

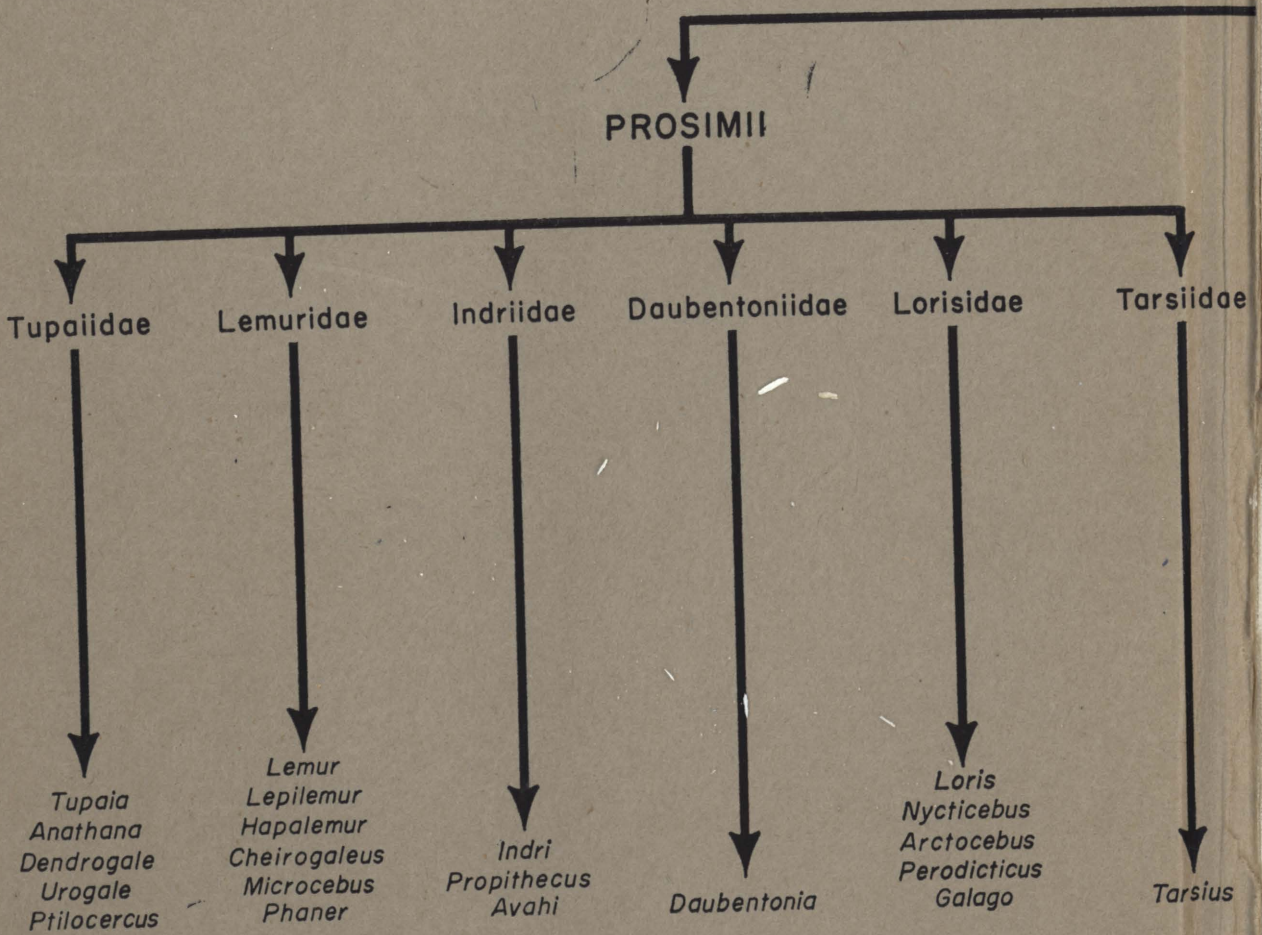
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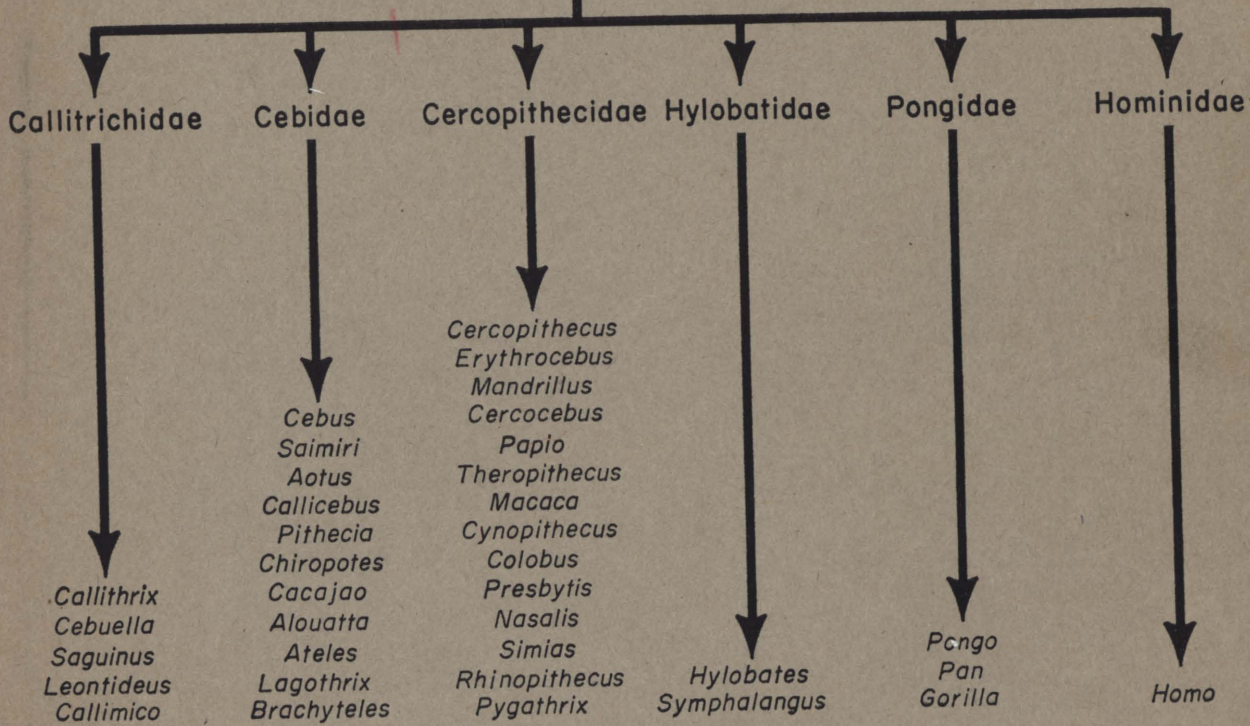
A Simplified Classification

PRIM



ATES

ANTHROPOIDEA



A
HANDBOOK
of
LIVING
PRIMATES



Papio ursinus, juvenile (by courtesy of C. K. Brain)

A
HANDBOOK
of
LIVING
PRIMATES

*Morphology, Ecology and Behaviour
of Nonhuman Primates*

J. R. NAPIER

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AND

P. H. NAPIER



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Preface

The idea for this book grew out of a collection of study notes for student classes on primate biology. During one annual revision, an impulse to extend and elaborate the notes resulted in the accumulation of a mass of data, which now constitute the skeleton of the present handbook. Just as study-notes can become handbooks, handbooks can grow into multi-volume monographs, a progression that we have tried to avoid by presenting the data in a systematic, concise, and, where possible, tabular form.

It is unlikely that the method we have chosen for presentation of the data will appeal to everyone. There are some, no doubt, for whom a reference book setting is an anathema. However, we have adopted this method simply because we feel that there is a great need among medical research scientists, human biologists and zoologists for the type of book where up-to-date, factual information on primate biology is readily available. The first handbook in this field, having a format not dissimilar to the present volume, was written by H. O. Forbes and published in Allen's Naturalists' Library in 1894. Until the publication during the last decade of W. C. Osman Hill's major treatises, Forbes' book was one of the few systematic accounts of the Primates in the English language; indeed it still serves as the principal *vade mecum* for many primate biologists.

As a result of the fervour to establish man's place in nature in the post-Darwin era of the 19th century, anatomists and zoologists gave the morphology of primates a thorough, if typological, going-over, and remarkably little can be added to their accounts of myology and osteology. On the other hand, animal behaviour, ecology and genetic biology, which today dominate basic research trends in primate biology, were unexplored fields. The sections on 'Habits' which embody behaviour and ecology in Forbes' Handbook rely wholly on the brief anecdotes of field naturalists. Today, our knowledge of the behaviour of free-ranging primates, though still desperately meagre in certain quarters, is increasing year by year as, happily, more workers enter the field armed with more and more generous grants.

In many ways primate biology is still in the "cataloguing and collecting" phase as it has been called; this must be regarded as an essential stock-taking exercise during which language and methodology develop and the bricks and mortar of the subject—the basic facts of primate taxonomy, morphology and behaviour—are collected and disseminated. Without these facts and without, at least, an awareness of the gaps in our knowledge, the subject cannot hope to fulfil its great promise. Basically this book is a catalogue of material, a collection of facts and a guide to deficiencies; but we hope it is a little more than that. Catalogues are not usually selective, they would hardly fulfil their purpose if they were. In the present handbook we have tried to avoid the mere propagation of unsifted and undigested fact by attempting a critical selection of the material. All that glisters is not gold—and primate biology possesses more than a fair share of lodes rich in iron pyrites. Where data are based on anecdotal, very limited or even single observations, we have introduced a note of caution by using the symbol *. To have omitted such limited data would have been to reduce the value of the handbook as even the most extravagant anecdote or unique observation may provide invaluable clues for further research.

In pursuance of the handbook principle we have adopted a shorthand style in the presentation of the data in Part II, which constitute the profiles for each genus. We have also used a numerical method of citing authorities. The authorities and dates of the relevant publications are to be found at the end of each profile; the full references are arranged alphabetically at the end of the book.



An alphabetical arrangement of profiles in Section II was selected in preference to a taxonomic one. We have also preferred to use the genus name as the principal heading for the profile rather than the familiar one. Familiar names show considerable regional variation, for instance the ubiquitous *Cercopithecus* of the *aethiops* group is known variously throughout Africa as the savannah monkey, the grivet, the vervet and the green monkey. Genus names, on the other hand, controversial issues aside, are as international as Linnaeus intended. A list of familiar names in common use in the English-speaking world, France, Germany and Holland, and their generic and specific synonyms appears in Section III. Vernacular names of purely indigenous usage are, for the most part, omitted. Common scientific synonyms are also listed in this section.

The taxonomy and nomenclature of primates, as no one will deny, are in a very fluid state; and as laboratory interest in these animals grows, and as more and more collecting and field study expeditions are set up, the confusion is bound to get worse before it gets better. Our principal aim in writing this book is to make primate biology as comprehensible to as wide a section of scientists as possible without indulging in the half-truths of over-simplification. Nowhere is this intention more difficult to realize than in systematics and nomenclature. It would be easy to accept the simplest classification available and to ignore the complicating emendations, however authoritative, on the grounds of expediency. But to adopt such a procedure is to misunderstand the aims of systematics which are not to provide merely a convenient *aide-mémoire* for the student, but to express in a biological, meaningful way the neontological and phylogenetic relationships between animal groups. If relationships between groups of primates should, on further study, turn out to be more complicated than was supposed, then one must accept any nomenclatorial complexities that result. Happily the trend deriving from the modern concept of species is on the whole towards "lumping" rather than "splitting"; however even a reduction of the number of genera and species can be as confusing as the addition of new taxa. Primarily we have based our classification on G. G. Simpson's "A Classification of Mammals" (1945) which is probably the best known and most widely accepted system in use today. But in a number of instances where this classification has seemed to us inadequate in the light of more recent knowledge, we have adopted the most *up to date and authoritative* work on the subject. In the face of conflicting opinions we have tended to follow the more conservative line believing that for the majority of primate biologists, stability of nomenclature is the most important consideration. Where nomenclatorial changes are sufficiently radical to warrant it, as in the case of marmosets and tamarins, we have included a table of synonyms. Where nomenclature is subject to current dispute we have tried to summarize both the problem and our own attitude towards it, in a Taxonomic Note to be found in Part III. In instances where genus names have been shown to be invalid on the grounds of non-availability we have followed the convention of including the rejected name in square brackets e.g. *Leontideus* [*Leontocebus*].

We did not set out to revise the taxonomy of primates; there are plenty of authors, bolder and better informed than we, who will do just this. We have only aimed to present the *facts* of primate biology in a comprehensible way and we believe that familiarity is the best framework for our intentions.

There is a mounting tide of opinion against the inclusion of the treeshrews among the primates. Van Valen (1965), in a palaeontological review, concludes that the tupaiid-primate relationship is "possible but unlikely". The posthumous paper of the embryologist J. P. Hill (1965) strikes heavily at one of the pillars on which this association rests—the characteristics of the placenta. Recent studies of the treeshrews, carried out at the Max Planck Institute by

Bob Martin (1966), argue against their inclusion on grounds of maternal behaviour. On the other hand there are a number of anatomical features, particularly in the dentition, the presence of a postorbital bar and other structural correlates of an advanced visual mechanism, that ally these forms closely with the primates. Goodman's (1962) evidence from immunological studies of serum proteins affines the tree-shrews with the primates rather than with non-primate mammalian groups. The situation with regard to the primate affinities of tree-shrews is equivocal to say the least. We have followed Simpson (1945), Clark (1959), Fiedler (1956), etc., in accepting their primate affiliations—however remote they may prove to be.

Part I of the book consists of an account of the morphology of primates; its purpose is to provide an overall survey of the principal functional characters which distinguish primates from the other mammals and from each other. Throughout this section, indeed throughout the book as a whole, we have tried to present the data with a proper balance between structure, function and behaviour.

In Part II the data for each genus are presented under several main headings; Geographical Range; Ecology; Morphology; Genetic Biology; Behaviour; Reproduction and Development; Captivity, etc. This sequence is pursued in Part III, the appendix, where explanatory notes will be found amplifying, discussing or defining terms and concepts used in the profiles of Part II; for example the vegetational zones and vertical classification of the forest canopy are discussed; and the differing types of primate locomotion and hand function are classified and defined.

In order to make it easier to compare certain characters of one genus with another, much of the quantitative data included in the profiles (e.g. weights, hand proportions, limb proportions, chromosome numbers etc.) are given collectively in tabular form under the appropriate sections in Part III.

It is not easy to write a book of this sort without making mistakes. These can creep into the text at any one of its many stages of preparation and, in spite of assiduous proof-reading, can appear shining like a beacon in its final published form. We have done our best to see that the unavoidable errors are kept to a minimum and that the avoidable errors, which are entirely the result of our own ignorance, are not too obtrusive. Having admitted the inevitability of error we can only apologize sincerely to those authors whom we have misquoted or misinterpreted and to those readers whom, thereby, we may mislead.

We are exceedingly grateful to a large number of friends and colleagues who have provided us with practical help. Without their generosity we could not have written this book.

J. R. NAPIER
P. H. NAPIER

May 1967

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PART I

Functional Morphology of the Primates

Erratum

Pages 249 and 251

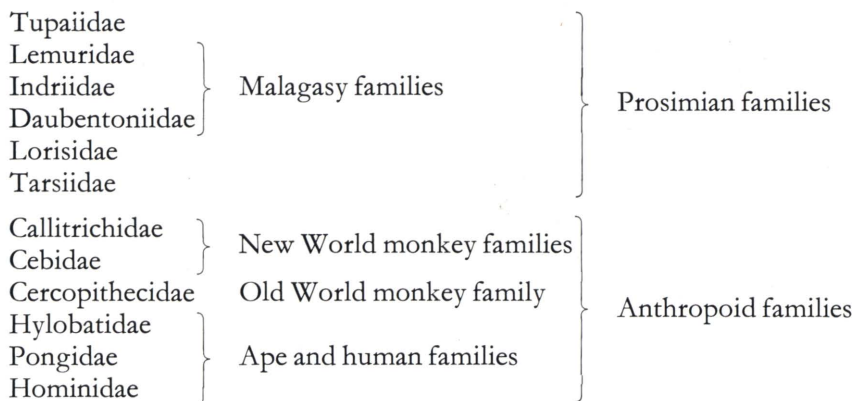
In legends for Plates 82 and 83, for
Papio cynocephalus read *Papio ursinus*

A Handbook of Living Primates

J. R. NAPIER and P. H. NAPIER

Functional Morphology of the Primates

From the point of view of their morphology the living primates are best considered in twelve natural groups or Families.



PROSIMIAN FAMILIES

1. Tupaïidae

This family comprehends the treeshrews which comprise five genera: *Tupaia*, *Dendrogale*, *Urogale*, *Anathana* and *Ptilocercus*. Geographically they are widely distributed throughout the Far East.

2. Lemuridae

A Madagascan family comprising *Lemur*, *Hapalemur*, *Lepilemur*, *Cheirogaleus*, *Microcebus* and *Phaner*.

3. Indriidae

This family includes the long-legged Madagascan lemurs—*Indri*, *Propithecus* and *Avahi*.

4. Daubentoniidae

A monotypic family comprising the aberrant Madagascan lemur *Daubentonia*, the Aye-aye.

5. Lorisidae

The family of lorises and galagos which has representatives in the Far East (*Nycticebus*, *Loris*) and in Africa (*Perodicticus*, *Arctocebus* and *Galago*).

6. Tarsiidae

A monotypic family containing the single living representative *Tarsius*. Tarsiers are found on many islands of the East Indies, e.g. Borneo, Philippines.



ANTHROPOID FAMILIES

7. Callitrichidae

South American family consisting of five genera of marmosets and tamarins, *Callithrix*, *Cebuella*, *Saguinus*, *Leontideus* and *Callimico*.

8. Cebidae

The largest family of South American monkeys comprehending all remaining genera, i.e. *Aotus*, *Callicebus*, *Pithecia*, *Chiropotes*, *Cacajao*, *Cebus*, *Saimiri*, *Alouatta*, *Ateles*, *Lagothrix* and *Brachyteles*.

9. Cercopithecidae

Monkeys of the Old World (Africa and Asia). An historically continuous family now subdivided geographically into *Presbytis*, *Nasalis*, *Simias*, *Rhinopithecus*, *Pygathrix*, *Cynopithecus* (Asia); and *Papio*, *Colobus*, *Cercopithecus*, *Erythrocebus*, *Theropithecus*, *Cercocebus*, *Mandrillus* (Africa). Only one genus *Macaca*, is common to both regions.

10. Hylobatidae

Lesser apes of the Far East ranging from Assam in the West to Borneo in the East. The family comprehends two genera: *Hylobates* and *Symphalangus*.

11. Pongidae

Great Apes of the Old World. Africa: *Pan* and *Gorilla*. South-East Asia: *Pongo*.

12. Hominidae

Represented by a single world-wide polytypic species, *Homo sapiens*.

The morphology of these 12 families link them together at ordinal level to form the Primates. The primate affinities of 10 out of 12 families are unequivocal, the two aberrant taxa being the treeshrews and the Madagascan genus *Daubentonia*, the Aye-aye. At one time, naturalists swayed by the morphology of the teeth included the Aye-aye with the rodents, but their primate affinities can hardly, now, be questioned. The treeshrews are still refused admittance by a number of authorities, notably W. C. Osman Hill. Certain authors (Evans 1942; Roux, 1947; Henckel, 1928) see difficulty in separating the treeshrews from the elephant-shrews in the Mentophyla section of the Insectivora on the basis of osteology. On the other hand, Clark on neurological (1932) and developmental (1959) grounds finds no such problem (but see J. P. Hill's (1965) posthumous paper on placentation in *Tupaia* and Campbell's (1966) preliminary note on the lamination of the lateral geniculate nucleus). Van Valen (1965) regards tupaiid-primate relationship as "possible but unlikely" on palaeontological grounds. Palaeontological evidence is equivocal but the morphology of living forms and, in particular, the evidence derived from serological techniques (Goodman, 1962a, b, 1963, etc.) still appear to be valid arguments in favour of retaining the treeshrews among the primates.

The list of families in the order presented, as well as being a horizontal section through a systematic scheme of living primates, also corresponds approximately to a *scala naturae* of primate evolution. The existence of a graded series among living primates recapitulating, in an approximate way, the phylogenetic stages of the fossil record, is a feature of the primate order that has been well-recognized since 1876 when T. H. Huxley wrote: "Perhaps no order

of mammals presents us with so extraordinary a series of gradations as this—leading us insensibly from the crown and summit of the animal creation down to creatures from which there is but a step, as it seems, to the lowest, smallest and least intelligent of the placental mammals.”

While such a state of affairs, unique among mammals, is most helpful to the primate palaeontologist, there is the constant danger that students will read into such a graded series, a linearity of descent that most certainly did not exist.* The graded series of living primates represents, as Clark (1959) has taken great pains to emphasize, the terminal products of many diverging lines of evolution. Stripped of their more obvious later specializations, they provide, however, a working model of the successive grades of organization in primate phylogeny from the lowest to the highest (Fig. 1).

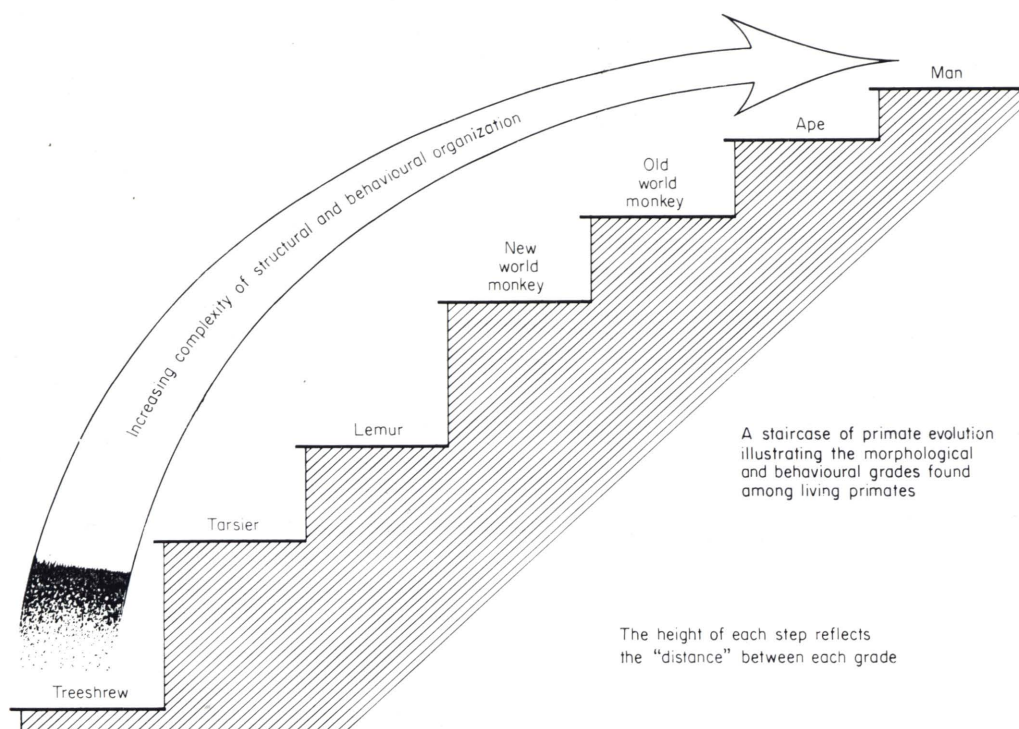


FIG. 1.

CHARACTERS OF THE ORDER

In 1873 St. George Mivart defined primates in the following terms:

“... an ungiculate, clavicate, placental mammal with orbits encircled by bone; three kinds of teeth at least at one time of life; brain always with a posterior lobe and a calcarine fissure; the innermost digits of at least one pair of extremities opposable; hallux with a flat nail or

* Students can hardly be blamed for falling into this trap which was so neatly and innocently set by Darwin in his “Origin” and so industriously placed in the path of the unwary by Huxley and Haeckel in their respective books. The erroneous concept of the “missing link”, the inevitable derivative of this way of thought, is the one “fact” that everybody thinks they know about evolution.

none; a well-marked caecum; penis pendulous; testes scrotal; always two pectoral mammae."

Professor F. Wood Jones in his book "Man's place among the Mammals" (1929) takes these criteria and examines them one by one; he concludes *à propos* of Mivart's definition "There is no single character . . . which constitutes a peculiarity of the Primates; for a primate animal may only be diagnosed by possessing an aggregate of them all" (p. 75). This important observation was also made by Clark (1959) who points out the difficulties of providing a clear-cut definition of the Order as a whole and observes (p. 42) that "There is no distinguishing feature which characterizes them all"—except a negative one, their lack of specialization. Clark supplies a list of evolutionary trends characteristic of the Order constituting a more useful and more meaningful diagnostic key than that provided by Mivart, whose definition does little more than supply a list of primitive mammalian features of which, to be sure, primates have a more than generous share. However, it must be remembered that Mivart was the first zoologist to attempt a comprehensive definition of primates that, *inter alia*, excluded the bats.

Clark's "evolutionary trends" are as follows:

1. Preservation of a generalized structure of the limbs with a primitive pentadactyly and the retention of certain elements of the limb skeleton (such as the clavicle) which tend to be reduced or to disappear in some groups of mammals.
2. An enhancement of the free mobility of the digits especially the thumb and big toe (which are used for grasping purposes).
3. The replacement of sharp, compressed claws by flattened nails associated with the development of highly sensitive tactile pads on the digits.
4. The progressive abbreviation of the snout or muzzle.
5. The elaboration and perfection of visual apparatus with development of varying degrees of binocular vision.
6. Reduction of the apparatus of smell.
7. The loss of certain elements of the primitive mammalian dentition and the preservation of a simple cusp pattern of the molar teeth.
8. Progressive elaboration of the brain affecting predominantly the cerebral cortex and its dependencies.
9. Progressive and increasingly efficient development of those gestational processes concerned with the nourishment of the foetus before birth.

Two further evolutionary trends may be added to the list:

10. Progressive development of truncal uprightness leading to a facultative bipedalism.
11. Prolongation of post-natal life periods.

The value of this key lies in its applicability to fossil as well as to living primates; with the exception of Trend 9, all the characters listed can be evaluated directly or indirectly from fossil material. Not *all* these trends are shown by *all* primates; nor do all primates show these trends to an equal extent. The overall judgment of affinity needs to be made not on the basis of the presence or absence of isolated characters but rather on total morphological pattern.

While essentially a morphological catalogue, Clark's list implies the acquirement of certain functional and behavioural traits that can be regarded as correlates of the structural ones. For instance, the preservation of a generalized structure of the limb skeleton can be interpreted in behavioural terms as the preservation of a generalized locomotor pattern that includes climbing, leaping and running, irrespective, for the most part, of the nature of the habitat. As an example of this inherent locomotor plasticity, spider monkeys which are in nature

among the most habitually arboreal of all Anthropoidea, can be maintained successfully in captivity in a totally "terrestrial" environment. Baboons and patas monkeys, on the other hand, in spite of extensive ground-living adaptations, remain sufficiently generalized to move and sleep in trees. Clark's second trend, interpreted in a functional and behavioural sense, can be considered in the light of the manipulative power of the hand and foot, the acquirement of an opposable thumb and big toe and independently mobile digits. Such behavioural characters as hand-feeding, grooming, tool-using and tool-making can be correlated with these functions in the hand, and certain locomotor specializations, particularly those shown by the anthropoid apes, with the analagous functions of the foot.

An automobile is composed of separate elements which, if properly assembled and supplied with a power source, will function on the test bench. So far so good, but it is not until the automobile is tested in its natural environment that the success or otherwise of the design can be judged. Only on the road can its behaviour be studied; and the best behaved cars are the ones the customers buy. Similarly, in nature, it is on behaviour that natural selection operates. Structure, function and behaviour are interdependent, and the success of an organism can be marred by imperfections at any one of these three levels; but whatever the underlying cause; the fate of an organism is finally decided by its behavioural responses to its natural environment.

In the following section, therefore, Clark's list of morphological trends in evolution are discussed principally in terms of their functional significance and behavioural correlations.

1. THE LIMBS AND VERTEBRAL COLUMN

All primates retain, in addition to a clavicle, a separate radius and ulna capable of the relative movements of pronation and supination which reach their maximal expression in the Hylobatidae, Pongidae and Hominidae. Apart from the Tarsiidae, in which the tibia and fibula are fused in the distal half of their length, a separate fibula is also a characteristic of primates (Barnett and Napier, 1953). All primates have five free digits on hand and foot with the exception of *Ateles*, *Brachyteles* and *Colobus* and certain of the Lorisidae. In *Ateles*, *Brachyteles* and *Colobus* the free thumb is secondarily reduced to a tubercle or is wholly absent; in these species however the metacarpal element is retained. A thumb markedly reduced in length and robustness is found in the Pongidae.

In the Lorisidae the 2nd digit of both hand and foot is considerably shortened; in certain Cercopithecidae also (e.g. *Theropithecus* and *Erythrocebus*) the 2nd digit is reduced in length. The carpal skeleton of primates, though subject to functional modification in the relative size of its components, is comprised of nine bones (including the pisiform and a single *os centrale*); the *os centrale* invariably fuses with the neighbouring scaphoid before birth in Hominidae and during post-natal growth in Hylobatidae and Pongidae; a fused centrale is also usually found in Indriidae, in some Lemuridae (*Lepilemur*) and occasionally in some Cercopithecidae (e.g. *Presbytis cristatus*). The tarsus varies little within the Order with regard to component bones, although considerable changes in relative proportions are seen (Schultz, 1963a). The primitive digital projection formula 3.4.2.5.1. for the hand, is retained tenaciously, the functional axis of the hand being the line of the 3rd digit; the only common variant of this formula (in Lemuridae, Indriidae and Lorisidae) is 4.3.2.5.1. or 4.3.5.2.1., the functional axis being shifted to the 4th digit.

4. MUZZLES, NOSES AND THE OLFACTORY SENSE

Broadly speaking the importance of the olfactory sense in primates is inversely proportional to the development of the mobility and sensitivity of the hands, as outlined in the last two sections, and to the evolution of overlapping visual fields to be discussed in the next.

The possession of a well-developed olfactory sense in some prosimian families is often used as an argument in favour of a ground-living origin for the primates, on the basis that a good sense of smell is of little advantage to tree-dwellers. However it is manifest that non-primate tree-dwellers, such as the squirrels, find plenty of reasons for retaining this special sense. It seems more likely that the debasement of olfaction in higher primates is an outcome of their *specialized* arboreality which has little in common with that of squirrels or any other tree-living Eutherian mammal.* The principal adaptations of primate arboreality are their manipulative and visual abilities. Improvement in these functions provided a much more effective—three-dimensional—means of exploring the environment than olfaction, which was thus gradually superseded as a prime sense. The morphological correlates of specialized visual and olfactory functions (the frontality of the orbits and a well-developed olfactory snout) are to some extent incompatible; in the Tarsiidae, for instance, the frontality and gross enlargement of the orbits have led to an actual physical compression of the nasal space: clearly, however, this is a special case.

The existence of a projecting muzzle or a strongly prognathic face in primates is not necessarily correlated with a highly developed sense of smell; nor is the presence of a complicated turbinal system wholly indicative of the importance of olfaction, for olfactory nerve-endings are not widely distributed over the mucous membrane of the nose but are rather strictly limited to the upper part of the cavity. A muzzle or snout may be associated with (a) a highly evolved olfactory sense as in Tupaiidae, or (b) an enlarged masticatory apparatus as in some Cercopithecidae (e.g. *Papio*) and some Pongidae (e.g. *Gorilla*), or (c) an enlargement of the larynx as in some Cebidae (e.g. *Alouatta*).

OLFACTORY MUZZLE

An "olfactory" muzzle is characteristic of certain Lemuridae and Lorisidae. The crucial factor which determines an "olfactory" muzzle in primates is not the length of the snout so much as the presence of a moist, naked rhinarium, curved nostrils, a naked philtrum and a tethered upper lip (strepsirrhine condition). In the majority of Cebidae the nostrils are wide apart (platyrrhine condition) but in the Cercopithecidae and ape and human families they are separated by only a narrow septum (catarrhine condition). The absence of a primitive type of philtrum allows the musculature of the face to spread across the upper lip and so facilitate its mobility; the mobile upper lip constitutes an important component of facial expression and vocal communication.

A progressive reduction in the importance of "marking" behaviour above prosimian level is associated with the debasement of the olfactory sense. The morphological basis of "marking" lies in the specialized cutaneous glands (allied to sweat glands) that are so prominent in Lemuridae and Tupaiidae. "Marking" behaviour is not wholly lost in anthropoid families, for

* Some Metatherian mammals such as the phalangers have become adapted to tree-life in a manner which is convergent with that of primates.

the Cebidae indulge in a form of urine marking similar to that seen in Lorisidae (Hill, 1957). Even in the Hylobatidae, Pongidae and Hominidae, although marking activity is absent, specialized glands are retained in certain regions of the body (e.g. in the axilla in *Homo*).

DENTAL MUZZLE

A "dental" muzzle is characteristic of certain of the ground-living Cercopithecidae, particularly the baboons* and the mandrills; in the latter genus the prognathism is exaggerated by the presence of striking paranasal bony swellings covered by highly coloured skin which appear to have little organic function and therefore, by default, are considered to be adornments having a social or sexual significance as signalling devices. Most of the remaining Cercopithecidae, the guenons and the colobine monkeys of Africa and Asia, are relatively flat-faced as are the Hominidae and the typical Cebidae (Plate 3). Among the Pongidae, the gorilla and the chimpanzee are the most prognathic; the orang-utan, *Pongo*, has a "dished" face that reveals that it is the forward growth of the upper and lower jaw that produces the prognathic effect seen in all great apes, rather than growth of the nasal bones, which in *Pongo* remain quite short. Likewise in the gelada baboons (*Theropithecus*) the face is moderately prognathic due to the presence of heavy jaws and large teeth but the nose is short and retroussé.

NOSES

Noses in the sense of an external nose consisting of nasal bones and fleshy and cartilaginous elements are not unduly obtrusive in the non-human primates; only among the colobine sub-family of Cercopithecidae and in Pongidae (e.g. *Gorilla*) are they remarkable. Among the Colobinae, both *Rhinopithecus* and *Simias* have short triangular-shaped tip-tilted or snub noses; in *Colobus*, on the other hand, particularly the black and white variety, the nose is rounded and overhangs the upper lip. However, it is in *Nasalis* that the colobine nose reaches its apogee; in the female the nose is triangular-shaped and projecting in profile view; in the male it is an enormously protuberant, fleshy organ that overhangs the mouth; the nares are completely inverted, opening on its undersurface. The external nose of *Nasalis* has no olfactory function; it has generally been regarded as a secondary sex characteristic. Functionally, it acts as an accessory vocal organ. The honking sound emitted by the adult male proboscis monkey owes its reverberating character to the resonating chamber effect produced by the nose. The nose is also used effectively by the male in threat display. The gorilla has a broad prominent nose formed by long nasal bones and by thickening and expansion of the alar folds; in this character it is clearly distinguished from most chimpanzees (except the occasional old male. Keith, 1899).

5. EYES AND VISION. EARS AND THE AUDITORY SENSE

The elaboration of the visual mechanism in diurnal primates is an adaptation to specialized arboreal life in which a high premium is placed on the ability to judge distances accurately in

* Scott (1963) points out that, in baboons, both dental and olfactory factors account for the prominence of the muzzle.

PLATE 3. Lateral view of the skulls of primates: a. Chimpanzee $\times \frac{1}{2}$; b. Gibbon $\times \frac{2}{3}$; c. Marmoset $\times 1$; d. Treeshrew $\times \frac{3}{4}$; e. Guenon $\times \frac{2}{3}$; f. Spider monkey $\times \frac{2}{3}$; g. Potto $\times 1$; h. Patas monkey $\times \frac{2}{3}$; i. Macaque $\times \frac{2}{3}$; j. Mouse lemur $\times \frac{1}{2}$; k. Baboon $\times \frac{1}{2}$. Scales approximate.



a



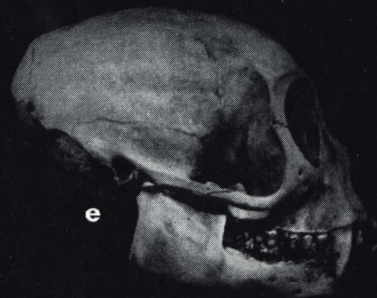
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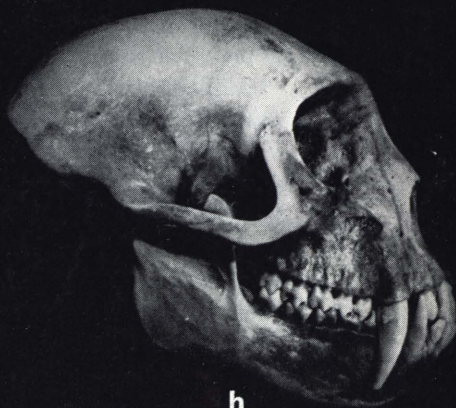
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(iii) an external auditory meatus is present in Tarsiidae, Cercopithecidae, Hylobatidae, Pongidae and Hominidae.

All primates possess ears potentially capable of being moved; this is true even in man. Mobility may be both intrinsic and extrinsic, or purely extrinsic. Intrinsic movement refers to the ability of certain primates—usually those of nocturnal habit—to fold the pinna on itself in a concertina-like fashion; extrinsic movement describes the ability to “scan” with the ears by altering their orientation with reference to the head. This function may be highly developed in certain nocturnal prosimian forms such as galagos or restricted to a simple retraction or flattening movement of very limited magnitude in the anthropoid families; broadly speaking primate ears can be classified into mobile and (relatively) immobile types.

The mobile ear is large, membranous and dish-like; on the inner surface of the pinna there are a number of alternating ribs and grooves that represent the sites of intrinsic folding which is activated by an intrinsic muscular system—the corrugator pinnae; the extrinsic muscles, both pre- and post-auricular in position are also well-developed. The mobile ear is most highly specialized in *Galago* and *Tarsius* and is seen in a less extreme form in some of the Lemuridae (e.g. *Microcebus*, *Phaner*) and in *Ptilocercus* among the Tupaiidae. All primate forms in which the highly mobile ear is found are nocturnal in habit. The diurnal treeshrew, *Tupaia*, possess a small rounded, relatively immobile and flattened pinna, reminiscent of the anthropoid ear. Clark (1959) observes that the subfamily that comprehends the nocturnal lorises (e.g. *Nycticebus*, *Loris*) possesses less specialized ears than the subfamily Galaginae; he suggests that this may be related to the differing requirements for temperature regulation in the slow-climbing lorises and in the rapid, energetic, leaping galagos.

The remainder of prosimian families and all the anthropoid families (including the nocturnal cebid *Aotus*) possess relatively immobile ears. They are generally small, oval or nearly circular in shape and show some degree of inrolling at their free edge. Mobility is largely extrinsic and varies considerably. Lemuridae show a moderate degree of protraction and retraction. Cercopithecidae show only retraction of a limited degree and in Pongidae the ears are practically immobile as they are in the Hominidae. Van Hooft (1962) has observed that among the Cercopithecidae the greatest degree of retraction is found in the wholly or partly ground-living genera (*Papio*, *Macaca*, *Mandrillus* and *Cercocebus*).

In addition to an auditory function, the ears of primates serve as signalling devices. In *Callithrix*, the variety of ear tufts and plumes of different form and colour constitute a highly visual means of species recognition. The role of the ears as components in communication through facial expression in anthropoid families has been discussed by Van Hooft (1962).

The external morphology of the ear is dealt with in a number of monographs by Pocock (1918, 1920, 1925a), and the musculature of the ear by Huber (1931). The malleus and the incus have been studied by Masali and Chiarelli (in press) with particular reference to the taxonomic position of the gibbons, which they find, in respect of morphometric characteristics, closer to the Cercopithecidae than to the Pongidae.

6. THE TEETH, DIGESTION AND DIET

A heterodont dentition consisting of incisors, canines and two sorts of cheek teeth is a primitive mammalian possession which has been tenaciously retained by all primates with the single exception of the dentally aberrant genus *Daubentonia*. The principal changes from the primitive mammalian dentition are a reduction in the *number* of teeth from 44 to 32 or 36, a

functional specialization in incisors and canines, and a modification of the cusp pattern of the cheek teeth.

DENTAL FORMULA

The primitive mammalian formula is assumed to have been: $\frac{3}{3} \frac{1}{1} \frac{4}{4} \frac{3}{3} = 44$. No living primates have retained three incisors in the upper jaw and the only family to have retained the 3rd incisor in the lower jaw is the Tupaiidae. The premolars have been reduced from four to three in the prosimian families and in New World monkey families; in the remainder—the Old World monkey, ape and human families—a further reduction to two has taken place. In the molar series the primitive number of $M. \frac{123}{123}$ is generally retained but there is a tendency among primates for the reduction or loss of the 3rd molar, thus:

Habitually absent: *Callithrix*, *Cebuella*, *Saguinus*, *Leontideus*.

Frequently absent: *Hylobates*, *Homo*.

Retrogressive changes: *Propithecus*, *Indri*, *Aotus*, *Callicebus*, *Saimiri*, *Cebus*, *Lagothrix*, *Ateles*, *Brachyteles*, *Callimico*, *Pan*, *Tupaia* ($M. \frac{3}{3}$ only): *Perodicticus* ($M. \frac{3}{3}$ only).

All the genera listed fall into the category of "short-faced" primates. The Cercopithecidae, a family which contains many "long-faced" genera, show the opposite trend, that is to say towards an enlargement of $M. \frac{3}{3}$. In addition the lower 3rd molar frequently bears a 5th cusp, (*Papio*, *Mandrillus*, *Colobus* etc., but not *Cercopithecus* or *Erythrocebus*). Long-faced monkeys constitute the more specialized group of the Cercopithecidae, at least as far as their jaws and dentition are concerned. Both *Gorilla* and *Pongo* (Pongidae) show a similar reversal of the trend, having $M. \frac{3}{3}$ often larger than $M. \frac{2}{2}$. *Pongo* even shows a high incidence of supernumerary molars. The less dentally specialized *Pan* and *Homo* show a common tendency for $M. \frac{3}{3}$ to be smaller than $M. \frac{2}{2}$. In *Homo*, $M. \frac{3}{3}$ are quite frequently absent. Agenesis of 3rd molar is reported to be greatest in Eskimoes (Moorees, 1957) and lowest in Negroes (Fanning, 1960). In white females Nanda (1954) found true agenesis in 9%. Among the Hylobatidae, the larger genus, *Symphalangus* shows no sign of reduction of $M. \frac{3}{3}$ while in the, relatively small gibbons (*Hylobates*) these teeth are frequently absent.

The Miocene fossil species *Proconsul africanus*, generally regarded as closely related to the ancestral line of living chimpanzees, shows retrogressive changes in upper 3rd molar (Clark and Leakey, 1951). *Proconsul africanus* was also a "short-faced" form as has been recently shown (Davis and Napier, 1963). All in all, it would seem that loss of $M. \frac{3}{3}$ is an evolutionary trend of the primate order, although certain specialized forms (principally the large ground-living primates) show a trend in the opposite direction.

INCISORS AND CANINES

Among the primates the anterior teeth are much less conservative in their morphology than are the cheek teeth. Their position at the front of the mouth, and hence their deployment for functions other than those concerned with seizing and chopping food, seems to offer a possible explanation for the variety of forms they display. The upper incisors show little variety although they tend to be small and peg-like in the prosimians (apart from *Daubentonia*) and broad and spatulate in the anthropoid families. In *Daubentonia* both upper and lower incisors are reduced to a single pair and have assumed a rodent-like shape and growth pattern. The lower incisors of certain Cebidae (e.g. *Cacajao*, *Pithecia* and *Chiropotes*) show procumbency

of a moderate degree, but it is in the prosimian families (excluding Tarsiidae and Daubentonidae) that extreme procumbency is found. In Lorisidae, Indriidae and Lemuridae, the lower central and lateral incisors, plus the canines, form a series of slender closely-packed, horizontally-projecting teeth which constitute the so-called dental comb. A similar, though less specialized, arrangement is seen in the treeshrews. The significance of the dental comb has been discussed recently by Buettner-Janusch and Andrew (1964) who regard it primarily as a grooming device; any alimentary function that it possesses is purely secondary.

Found under the tongue in lemurs and lorises is a horny denticulated structure, the sublingua. This structure is functionally associated with the dental comb and has been aptly described by Clark (1959) as a "toothbrush"; its principal function being to rid the comb of hairs and debris. The sublingua is vestigial in the Anthroidea being represented by a fold of mucous membrane, the plica fimbriata.

The canines show considerable variation in primates in respect of size, shape, projection and degree of interlocking; the canines also show sexual dimorphism in certain genera. Apart from the Hominidae, all families show some degree of projection of canines beyond the tooth row; this is usually more pronounced in the upper jaw than in the lower. Even in man the upper canines may project below the occlusal surface of the tooth row to a greater degree than the lower canines. The degree of projection and stoutness of the tooth varies considerably, particularly among the Cebidae. *Callicebus*, for instance, shows relatively little projection while in *Chiropotes*, the canines are long and extremely stout. The longest and sharpest canines are found among ground-living Cercopithecidae; and the most massive among the Pongidae.

The occurrence of sexual dimorphism in canine size in Cercopithecidae and Pongidae suggests that their prime function, (and therefore their significance in natural selection) is not wholly alimentary. However there is no doubt from the massive form and from the evidence of wear in the *Gorilla* for instance, that they are not mere adornment: and are probably used by this animal for stripping bark. The slender, dagger-like canines of baboons (which being vegetarians have no need for carnivorous adaptations) have a non-alimentary function which would appear to be associated with the rôle of the male in the social organization of the troop. In baboon troops the dominant male controls the troop, limits intra-group fighting and protects the young; all these functions are performed with the minimum of actual aggression; the threat of aggression being the principal device. When troop relationships are stabilized, even threat is rare (Hall, 1964). Threat also operates in predator defence, an aggressive display by large males being very often sufficient to discourage attack by cheetahs or leopards. These remarks apply equally to the macaques, a genus in which sexual dimorphism in canine size (as well as body size) is also striking. Some families, such as the Hylobatidae, show little or no sexual dimorphism in canine (or body-) size. The social structure of gibbons and siamangs is based on the family unit rather than on the troop and it would seem that a different explanation for the large canine size of Hylobatidae is required. Carpenter (1940) found little evidence of inter-group aggression in wild populations of gibbons although recent observations of Frisch (1963) on the frequency of broken canines in gibbons suggest that fighting between different groups does occur and that the males are the protagonists. New light has been thrown on the territoriality of one species of gibbon, *Hylobates lar*, by the field observations of Ellefson (in press) who describes inter-group aggression as commonplace leading not infrequently to actual physical encounters between males.

Other aspects of primate behaviour such as communication through facial expression need

to be studied, to understand this aspect of the role of the front teeth; there is little doubt that the grin-face of most primates, the "snarl" of the baboon and mandrill and the smile of man as well as other expressions that expose the teeth, such as yawning, are displays of profound significance for primate communication.

PREMOLARS AND MOLARS

The evolutionary trend in both the molar and premolar series has been to increase the number of cusps, though primates may be regarded as the most conservative of mammals in this respect. The primitive premolars are homodont and unicuspid; in non-human anthropoid families, with the exception of the anterior lower premolars, they are bicuspid, an additional medial cusp having been derived from the cingulum. The anterior lower premolar in Cercopithecidae and Pongidae is a unicuspid tooth modified to form a shearing surface against which the upper canine plays; this type of tooth is usually referred to as sectorial.

In Hominidae, both fossil and living, both upper and lower premolars are homodont and bicuspid.

In prosimian families on the whole a unicuspid condition prevails but in this group the anterior and posterior premolars tend to become specialized away from the typical premolar form. The anterior premolar assumes a caniniform form and function in certain Lemuridae (e.g. *Phaner*, and to a lesser extent in *Lepilemur*) and the posterior premolar becomes molarized in Lorisidae and Tupaiidae, though not in Lemuridae or Tarsiidae.

The primitive Eutherian condition of tritubercular upper molars, with a raised trigone and a talon basin persists in Tupaiidae and Tarsiidae. The evolutionary trend in primates as far as the *upper molars* are concerned, is the development of a true hypocone. In the Lemuridae and Indriidae several stages of this metamorphosis are seen: the molars are tritubercular in Cheirogalinae; they present an incipient hypocone in *Lemur* and *Hapalemur*; a hypocone is present on M.² in *Lepilemur* and *Phaner*, and full quadritubercular status is shown by Indriidae. The Lorisidae also show four cusps although the size of the hypocone varies from genus to genus.

Among the anthropoid families, only Callitrichidae retain tritubercular molars; all other families show the quadri- or quinetubercular condition. In Cercopithecidae the upper molars show marked waisting between anterior and posterior pairs of cusps; each pair of cusps is united by a strong transverse ridge (bilophodont condition). The dentition of the gelada baboon shows these characteristics in a most exaggerated form (Jolly, 1964). In the ape and human families, there is no bilophodonty; instead the antero-internal and postero-external cusps are joined by an oblique ridge (a similarly disposed ridge is also found in the New World genera *Ateles* and *Alouatta*).

The trend in the *lower molars* has been towards a modification of the original trigonid by the loss of one cusp (paraconid); the elevation of the talonid basin until the occlusal surfaces of trigonid and talonid are level; the enlargement of the talonid cusps (hypoconid and entoconid) to form a quadricuspid tooth; and the development of a 5th cusp, postero-lateral in position—the hypoconulid. The quadricuspid lower molar is seen in all Prosimian families, other than Tupaiidae and Tarsiidae; it is also seen in the Cebidae, Callitrichidae and Cercopithecidae. In the Pongidae the lower molars bear five cusps (Y₅ pattern) and are further distinguished from those of Cercopithecidae by the absence of bilophodonty. Most genera of Cercopithecidae have a fifth cusp on the talonid of M.₃, the exceptions being *Erythrocebus* and *Cercopithecus*. In the human family the quadricuspid condition (+ 4 pattern) is often seen.

DIET AND DIGESTION

The relationship between tooth form, alimentary tract morphology and diet in the primates is not a very obvious one. Hill (1956b) listed the vegetable and animal components of primate diet in an arboreal environment:

Vegetable: Fruits, flowers, leaves, bark, pith, seeds, roots, tubers and nuts.

Animal: Birds, birds' eggs, lizards, spiders, insects, frogs and crustacea.

To extend this list to embrace the diet of ground-living, extra-forest forms, one would need to include grasses and small mammals. Both the patas monkey (*Erythrocebus*) and the baboon (*Papio*) include large quantities of grass in the staple diet; in the latter genus, occasional meat-eating is well established (Dart, 1963; Washburn and De Vore, 1963; De Vore, 1965). Recent evidence from field studies (Goodall, 1963) reveal that the eating of freshly-killed meat is occasionally observed in chimpanzees. The general impression gained from reports of meat-eating among primates is that it is very much an *ad hoc* affair, a matter of learned behaviour. This view receives support from the fact well known to zoo authorities that primates in captivity, even *Gorilla* which is a strict vegetarian in nature, will readily eat meat if presented (Crandall, 1964).

Generally speaking, primates are omnivorous: relatively few of them are restricted in diet and none are restricted to the extent found in some non-primate mammals such as for instance the koala bear and the giant panda. The leaf-eating monkeys and certain of the lemurs are probably the only primates which can be regarded as having a narrowly specialized diet in the wild. Leaf-eating monkeys include the Asian langurs and African colobus monkeys (Colobinae), *Alouatta* (the howler monkey) and the Madagascan family, Indridae. In captivity,

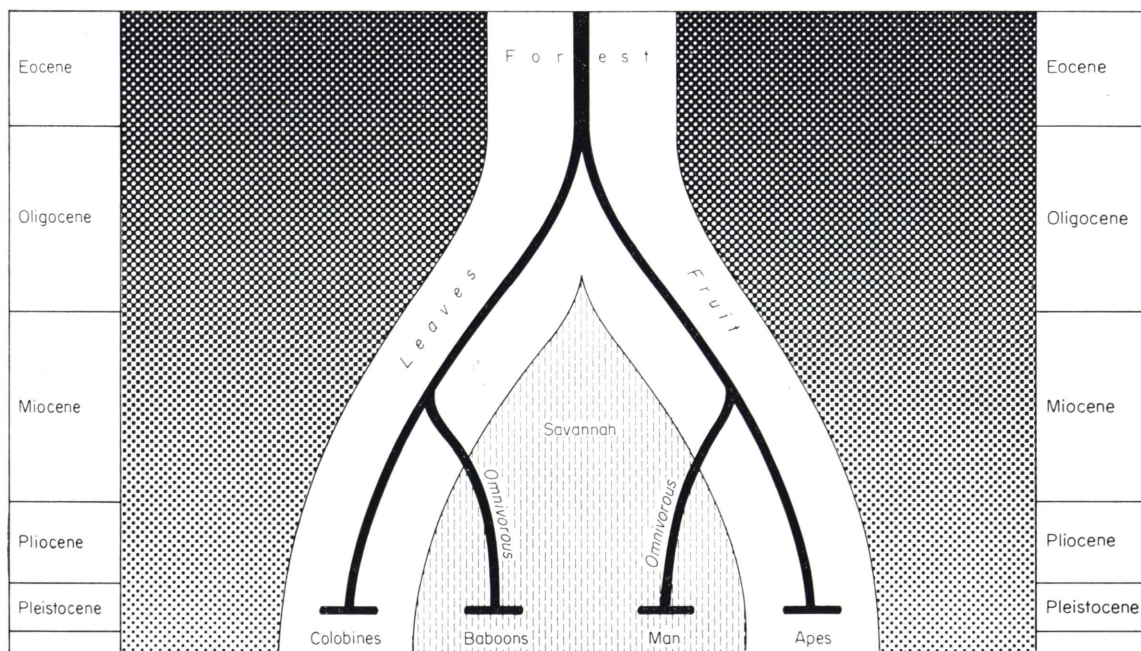


FIG. 2. Diagram illustrates the hypothesis of an early dichotomy of catarrhine primates on the basis of specialized diet. Secondary occupation of a savannah niche by progressive Cercopithecoidea (leading to modern baboons) and progressive Hominoidea (leading to modern man) was accompanied, *inter alia*, by adoption of an omnivorous diet.

colobs, langurs and howler-monkeys do well on fruit and vegetables. The aberrant aye-aye (*Daubentonia*) is largely insectivorous but also eats fruit; galagos may be largely insectivorous in the wild. Some of the Pitheciinae (*Pithecia*, *Chiropotes*) are reported to be wholly frugivorous as judged from stomach-content analysis (Fooden, 1964b).

In primates dental adaptations to diet, as might be expected from this lack of specialization, are not particularly obtrusive. The most extreme behavioural adaptation is that of *Daubentonia* which adopts a rodent-like gnawing action for excavating wood-boring insects. Other adaptations that can be correlated with the diet are the large size of the molar series in *Gorilla* which is a bulk vegetarian, the sharply-pointed molar cusps of *Tarsius*, *Aotus* and *Galago* etc. related to their largely insectivorous habits; and the unique form of upper and lower molars in the leaf-eating howler monkeys. Other striking dental characters such as the broad spatulate upper incisors of Pongidae and the bilophodont pattern of cercopithecoid molars may also be dietetic specializations; these dental characters may indeed be of considerable phylogenetic significance indicating a separation of the early catarrhine primates into two main ecological types; fruit-eaters and leaf-eaters. Although these dietary distinctions are somewhat blurred in modern catarrhine families as a result, it is presumed, of secondary ecological shifts, the ancient dichotomy is still apparent between the leaf-eating Colobinae and the fruit-eating Pongidae and Hylobatidae (Fig. 2).

DIGESTIVE SYSTEM

A similar lack of specialization is seen in the alimentary systems of primates. Characters of the visceral system thus provide important evidence, as do the teeth, of phylogenetic relationships within the Order. Adaptive changes in the alimentary tract, which can satisfactorily be correlated with diet, affect principally the stomach, the caecum and the colon. Among leaf-eaters, for example, the stomach is large and shows some tendency towards sacculization (particularly in Colobinae); the caecum and colon are voluminous. Defaecation patterns vary considerably with the nature of the diet. Highland gorillas which are bulk eaters defaecate five or six times a day whereas the Western race, whose diet contains a higher proportion of fruit, seldom defaecate more than once daily. This physiological difference may probably be correlated with the observation that nests of Western gorillas are usually free of excreta; the highland race almost invariably foul their nests.

Leaf-eating primates also exhibit large salivary glands. Cheek pouches, another adaptation that might loosely be regarded as alimentary, are seen in the family Cercopithecidae; these capacious extensions of the cheeks that extend below the ramus of the mandible to meet almost in the midline, are crammed with food which is then pushed back into the mouth by hand, chewed and swallowed at leisure. It has been suggested that cheek pouches have much the same physiological function as the modified stomachs of leaf-eating monkeys, thus either one or other are present in catarrhine monkeys but not both. While the latter fact is undoubtedly so, the suggested analogy seems unlikely; there is no indication that digestion is occurring while the food is held in the cheek pouches; and recovery from cheek pouches can not really be regarded as analogous to the regurgitation of ruminants. Furthermore, leaf-eating monkeys never ruminate or regurgitate their food (Ayer, 1948). The leaf-eating stomach is not comparable to the ruminant stomach but is merely an exaggeration of the typically tripartite primate stomach. The adaptive significance of cheek pouches is not at all easy to understand; they occur throughout the Cercopithecinae (but are absent in Colobinae) and therefore must be presumed to be a relatively recent possession. Their survival value to modern cercopithecines,

many of whom obtain their food by raiding native plantations, is obvious, but it is not so easy to see their significance for past populations. This feeding habit however may indicate that in the past the Cercopithecinae were more ground-living than they are today. Cheek pouches would be a highly advantageous adaptation for monkeys living at the forest edge or in a forest-savannah mosaic type habitat and foraging in open savannah.

Tomes (1923) pointed out that there was less variation in the teeth of primates than in their diet. The validity of this statement is questionable, for the diet, with few exceptions, is remarkably homogeneous from the point of view of composition and consistency, and the teeth show a great many adaptive specializations within the framework of the generalized primate dentition. Not all these adaptations however are related to diet (*vide supra*). The teeth would undoubtedly have shown greater adaptation to such dietary differences as exist, were it not for the early differentiation of the forelimbs as prehensile organs. Hands which are capable of seizing food, manipulating and breaking it up, can take over effectively many of the functions that in mammals without specialized hands, are performed by the teeth. Food which is picked by hand does not require to be bitten off; and food which is torn apart in the hands requires less mastication. Man, as a result of his cultural advances in the use of fire for cooking and tools for eating, has now taken the process one stage further by relieving even his hands of these responsibilities.

JAW SIZE

Generally speaking among the primates the expansion of the brain and thus of the brain case, and the reduction in jaw size associated with a secondment to the hands of some of the food-getting functions of mammals, has made unnecessary the addition to the skull vault of a sagittal crest for the hypertrophied jaw muscles. The neurocranium supplies a sufficiently wide area of attachment for the temporalis muscle in most primates to obviate the mechanical need for a sagittal crest. In larger primates such as baboons, gorillas and oranges which possess heavy jaws, sagittal crests are commonly seen in the male and only rarely seen in females. It is well known that whereas the relative size of the brain case *decreases* as the absolute body size of an animal *increases*, the relative size of the jaws increases with the body size. In the skulls of large monkeys such as baboons and mandrills the brain-case looks relatively small compared with the facial skeleton; the reverse is true in small monkeys such as talapoins. This is an expression of allometric growth. It has been shown that there is a constant relationship between body size and facial length in *Papio* (Freedman, 1957, 1962; Jolly, 1964); this correlation is independent of sex however. Because of the sexual dimorphism which exists in baboon populations, the longest faces (and therefore the largest sagittal crests), naturally, are found in males. The combination of relatively large jaws and relatively small neurocrania makes the provision of additional bone surface obligatory for attachment of the jaw musculature. In chimpanzees a very low sagittal crest is occasionally found in males but only very occasionally in females (Ashton and Zuckerman, 1956); this may be attributed to the relatively small size of chimpanzees compared with gorillas, to their essentially frugivorous diet and to the somewhat retrogressive nature of the third molar tooth. Ashton and Zuckerman (*loc. cit.*) found low crests in male *Cercopithecus ascanius*. Small crests in the region of the lambda are also seen in male *Colobus*. In fact they can be found in any primate that possesses large jaws and a small braincase although, for reasons stated above, there is a tendency for these adaptive features to be found most often in the larger species. The position of sagittal crests on the vault of the skull depends on the degree of prognathism of the face and the arrangement of

the fibres of the temporalis muscle. In *Papio* in which the snout is strongly developed, the posterior oblique element of the fan-shaped temporalis muscle is larger than the anterior-vertical component. Thus, the crest appears first in—and may be limited to—the region of the lambda (Jolly, 1964). In *Theropithecus*, a baboon-like primate but with a less prominent snout, the crest extends further forward to the region of the bregma.

The occurrence of the nuchal crest, and raised flange of bone in the occipital region is largely (though not wholly) related to the postural adaptations of the skull, and is discussed in Section 9.

The following table lists the average body weight of male and female anthropoid apes. Figures are also given (Schultz, 1956) of the average body weight of females in percentage of the average body weight of males. These comparative figures may serve to rationalize the presence or absence of sagittal crests in these hominoid genera.

TABLE I

	Average weight adult male	Average weight adult female	♀ weight in % ♂ weight	Sagittal crests
Chimpanzee	49 kg	41 kg	84%	Occasional low crest in male (16%). Only very occasionally in female
Orang-utan	79 kg	37 kg	47%	Large in male. Rarely in female
Gorilla	160 kg	92 kg	58%	Large in male. Occasional occurrence in females (30%)

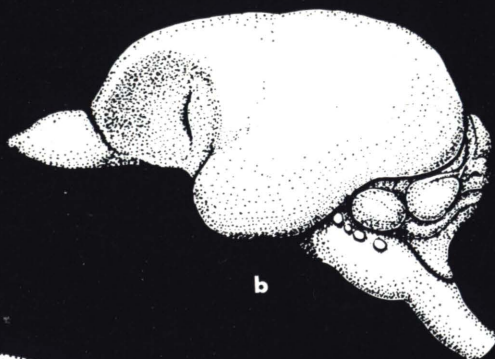
7. THE BRAIN

The wholly imaginary hippocampus minor, the subject of a major scientific bloomer of the post-Darwinian era, and the *vera causa* for a delightful parody in "The Water Babies", serves as a trenchant reminder that no new structure is to be found in the human brain that is not found in the brain of other primates. The differences between the brains of the highest and lowest of the primate grades lie, principally, in the progressive elaboration, differentiation and reorganization of the cerebral cortex and cerebellum (Plate 4). Many of the modifications are linked with the development of an advanced visual system and with the evolution of prehensility, opposability and tactile acuity in the hand (Noback and Moskowitz, 1963).

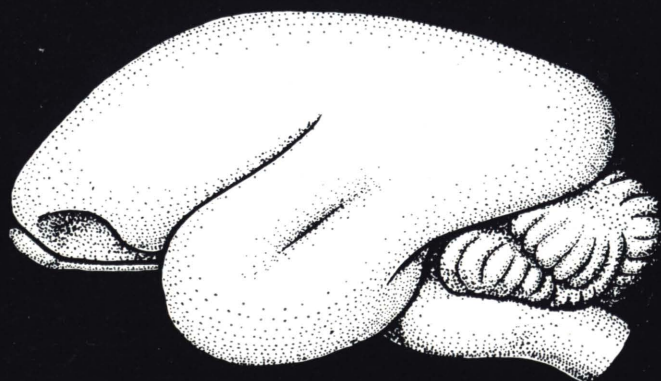
Treeshrews are still classified by some authorities with the elephant-shrew in the Menotyphla division of the Insectivora but in the development of the neopallium these forms differ profoundly from each other (Clark, 1932b). The brain of the diurnal *Tupaia* is large for its body size and, by comparison with certain insectivores such as *Echinosorex* (a nocturnal form), the olfactory bulbs, tracts and tubercles are reduced. The piriform lobe is largely concealed by the growth of the temporal lobe of the neopallium; the visual cortex is expanded to cover the mid-brain and part of the cerebellum. There are no sulci on the lateral surface of the hemisphere but a small calcarine sulcus, delimiting the visual cortex, is apparent on the medial side. Associated with these external cortical changes, there is a differentiation of cellular elements of the striate cortex and of the thalamic nuclei (Clark, 1929). Correlated with the lack of



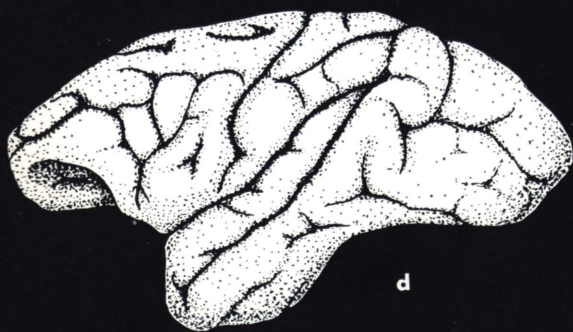
a



b



c



d



e



f

frontality of the orbits of *Tupaia*, there are no uncrossed fibres in the optic chiasma (cf. *Tarsius* 25–35% uncrossed fibres; Cercopithecoidea 40%; Hominoidea 40%. In all these, orbital frontality is fully established).

The brain of Lemuridae is known principally from the work of Clark (1931) on *Microcebus* which shows the most primitive condition of all Lemuriformes. In many ways *Microcebus* shows little advance on the tupaiid brain. The olfactory lobes are relatively large in all Lemuridae and the piriform lobe of the cortex, as in *Tupaia*, still forms the lower pole of the temporal lobe; in *Lemur*, however, it has become completely concealed. The occipital lobe of *Microcebus* remains relatively unexpanded and the posterior horn of the lateral ventricle is absent; the visual area of the cortex however is larger than in *Tupaia* though it still extends well on to the lateral surface of the hemisphere. A retrocalcarine sulcus, characteristic of all primates above tupaiid level, is in evidence on the medial surface of the cerebral hemisphere. The lateral cerebral surface of *Microcebus* shows a lateral sulcus but is otherwise lacking in fissures; in *Lemur* several longitudinal sulci are apparent; in Indriidae the cortex shows the most complex fissural pattern among the Lemuriformes. It must be remembered however, in this respect, that the complexity of fissural patterns of cerebral cortex are correlated with size. In other mammalian Orders e.g. Perissodactyla, increased fissuration has evolved hand in hand with increase in body size (Edinger, 1948).

In terms of cyto-architectonics, the cortex of Lemuridae shows considerable advances on that of the Tupaiidae, particularly in the primary projection areas and to a lesser extent in parietal and temporal association areas: these latter regions are concerned with the storage and integration of all sensory memories (visual, tactile, auditory, etc.). In the thalamus, the lateral geniculate nucleus has become elaborated in connection with the increasing importance of the visual mechanisms; in lemurs, the lateral geniculate nucleus shows a distinct lamination of the cellular layers. The lamination is somewhat irregularly displayed in *Tupaia* and inversion is absent. In the anthropoid families, similar lamination and differentiation of the lateral geniculate body has occurred, but the pattern is quite different, the whole nucleus becoming rotated ventrally and “everted” (Clark, 1932a; Chacko, 1955).

In many ways the brain of *Tarsius* is less advanced than that of *Microcebus* despite its apparent anthropoid-like contour (Plate 4b). This is due principally to the size of the visual cortex which produces a prominent occipital pole, and to the reduction in the olfactory apparatus. The cerebral hemispheres lack any surface fissural pattern except a short lateral sulcus and a deep calcarine sulcus. As might be expected from the size of the visual cortex, the lateral geniculate nucleus is large and shows laminated differentiation of the “inverted” or lemuroid type.

In view of the specialized locomotor functions of *Tarsius*, which involve precise leaps from vertical support to vertical support, it is surprising (Clark, 1959) that the cerebellum lacks the enlargement and fissuration of the lateral lobes that might well be expected. An increase in the fibre connections between cerebrum and cerebellum, which facilitates muscular co-ordination, is reflected in the size of the cortico-pontine-cerebellar tracts, the size of the pontine nuclei and in the size and differentiation of the lateral cerebellar lobes. Elaboration of this system is a progressive feature seen in the ascent from lower to higher primates.

The simplest brain among the Anthroipoidea is found in the Callitrichidae. Even so it is far in advance of the brain of prosimian families, being relatively very large compared with body

PLATE 4. Brains of primates. Lateral aspect of cerebral hemisphere of: a. Treeshrew $\times 3$; b. Tarsier $\times 2\frac{1}{2}$; c. Marmoset $\times 2\frac{1}{2}$; d. Macaque $\times 1$; e. Gorilla $\times \frac{1}{2}$; f. Man $\times \frac{1}{2}$ (a, b, c, and e after Le Gros Clark, 1959). Scales approximate.

weight (Plate 4c). The olfactory parts of the brain are more reduced than in the prosimians and the visual parts (Tarsiidae excepted) are more advanced. The common marmosets (*Callithrix*) show little or no fissural patterning of the cerebral cortex beyond a lateral sulcus and in a calcarine system, but the larger representatives of New World anthropoid families, e.g. Cebidae, possess a richly convoluted cerebrum. *Cebus*, for example, shows a number of vertically orientated and arcuate sulci (cf. the longitudinal arrangement of sulci in the larger Lemuridae). As in all the Anthropeoidea, the lateral geniculate nucleus of *Callithrix* is of the everted type.

CEREBRAL CORTEX

The expansion of the cerebral cortex, characteristic of the Anthropeoidea, is a result of two factors; firstly, an increase in the size of ascending and descending fibre tracts that connect the cortex with sub-cortical centres and the spinal cord; secondly an elaboration of the association areas and of the intrinsic fibre systems that connect them with the primary motor and sensory projection areas on the same and opposite sides of the brain. The primary motor projection area constitutes both the pre-central gyrus and the area immediately anterior to it. The primary sensory areas are those areas of cortex related to vision (occipital), hearing (temporal) and general sensation (parietal). The remainder of the cortex consists of association areas whose function is concerned with the storage of acts or sensations learned and remembered.

The manipulative power of the hand and its role in sensory acuity, is reflected both in the size of the relevant motor and sensory association areas, and in the cortical representation of the hand in the primary motor and sensory projection areas. The size of the specific area of cortical representation for the hand, determined by means of neurophysiological experiment, forms an ascending series in Callitrichidae, Cebidae, Cercopithecidae and Hominidae (Noback and Moskowitz, 1963). The expression of the primate trend towards a higher functional differentiation of the brain (corticalization) is a concept whereby the cortex assumes the dominant role over the lower centres. The relative extent of corticalization in anthropoid families is apparent following selective cortical ablations in monkeys, chimpanzees and man. Ablation of the primary motor area of the cortex in Pongidae leads to more severe and more persistent ill-effects than in Cercopithecidae, and in Cercopithecidae than in Cebidae; the brunt of the disability falling on skilled motor acts. Ablations of the sensory cortex result in severe impairment of discriminatory functions which are more affected in man than in the chimpanzee, and in the chimpanzee than in the monkey.

During primate phylogeny, it would seem that with the evolution of the Anthropeoidea a plateau was reached with respect to visual mechanisms. Studies of recent anthropoid families do not indicate any profound qualitative differences in the structure of the visual pathway. It is true that differences exist in the lateral geniculate body, in the number and arrangement of the laminae and in the ratio of cells and neurones between monkeys (Cercopithecidae, Cebidae) and the ape and human families, which suggest refinements in vision, particularly peripheral vision (Noback and Moskowitz, 1963). Differences also exist in the boundaries of the striate area in the occipital lobes. In the Cercopithecidae, most of the striate area is sited on the lateral surface of the occipital pole whereas in man, and to a lesser extent in the Pongidae, it is largely confined to the medial surface, lining the depths of the calcarine fissure; this displacement is presumably brought about by an expansion of parietal, occipital and temporal association areas among the higher primate grades that have resulted in an "infolding" of the occipital pole.

The external morphological correlates of a highly evolved visual sense, the frontality of the

orbits and the development of a post-orbital closure, are already apparent in the fossil catarrhine frontal bone discovered in the Fayum of the Egyptian Lower Oligocene. This bone has been attributed provisionally by Simons (1962) to *Oligopithecus*. An enhanced visual system would thus seem to have been established early in catarrhine phylogeny. The central nervous correlates of manipulative ability and sensory acuity of the hand however, show a progressive "improvement" through the anthropoid grades from Cebidae to Cercopithecidae, to Pongidae, to Hominidae. This "improvement" which is apparent in living forms, accords well with the palaeontological evidence, which suggests that the total emancipation of the hand from the function of weight-bearing and its secondary deployment as a tool-using and tool-making device was a relatively recent event in primate evolution.

Holloway (1966), in a stimulating review of the significance of cranial capacity as a parameter of hominization, points out that the comparison of cranial capacities between man and sub-human primates is nonsensical (*sic*) in as much as it is not based on the comparison of equal units. That is to say, 1 cc of chimpanzee cortex is not equivalent to 1 cc of human cortex. Anatomical studies have shown that cell density *decreases* as brain size increases (Tower, 1954). This may be due to an increase in size of the nerve cells themselves, or an increase in dendritic branching, or even an increase in neuroglial cells (Hawkins and Olszewski, 1957). Thus a fourfold increase in brain size, for instance, does not mean that there are four times as many neurones. Holloway (*loc. cit.*) suggests that the essential differences between the brains of lower and higher primates is a matter of neural reorganization. He states (p. 106) that "quantitative shifts between components or substructures of the brain, as measured in terms of area or volume, have taken place under natural selection such that the outputs of the systems are different between species. By shifting interactions between components in quantitative ways, the product of the whole is altered."

At sub-cortical level attention has centred on the limbic system and particularly on the amygdaloid component of the rhinencephalon. The importance of the amygdala for olfaction still remains uncertain; for instance in the human brain, in spite of the phylogenetic debasement of olfaction as a sensory function, the amygdala remains large as it does indeed in anosmatic mammals like the porpoise. Stimulation experiments in animals and ablative operations in man produce conflicting evidence of the extent of the primary olfactory representation in the amygdala. The amygdaloid nucleus, however, is clearly involved in some way, at present unknown, in the expression of the rage reaction. Bard and Mountcastle (1948) showed, in the cat, that there was a marked depression of the rage threshold following bilateral amygdalectomy.

Experimental evidence seems to point to the amygdala and other parts of the limbic system as being modulatory in function. Rothfield and Harmon (1954) showed that placidity resulted from experimental neocortical ablations in animals providing that the limbic system was left intact. If the fornix fibres were severed, the rage threshold was lowered; the modulatory function of the limbic system was thus reduced. The effect of the disturbance produced by these lesions on those mechanisms which normally allow the selection of a behaviour pattern adequate for a given situation, was to produce an indiscriminate and inappropriate rage reaction.

In direct contrast to the findings of Bard and Mountcastle (1948), the bilateral excision of the amygdala in monkeys has been shown to alter the relative hierarchical positions of a group of male rhesus monkeys, previously dominant individuals becoming peripheral (Rosvold *et al.*, 1954). Chance (1962) has discussed the evolution of the amygdaloid nucleus in primates with particular reference to the genesis of the rage-controlling ability of man. The results of

amygdalectomy in man however are as equivocal as they are in animals (see Gloor, 1960). Changes for the worse in maternal behaviour of female monkeys has also been noted after bilateral amygdalectomy (Thomson and Walker, 1950; Walker, Thomson and McQueen, 1953).

Attention of anatomists and physiologists has also been directed to the fornix-mamillo-thalamic system. Simpson (1952) and Daitz (1953) counted fornix fibres in monkeys and in man and their results show a fourfold increase in the fibres of the human sub-callosal fornix over the macaque. Powell, Guillery and Cowan (1957) demonstrated the relatively large size of the human fornix-mamillo-thalamic system compared with that of *Macaca mulatta*, and conclude that this system plays a "relatively important, though unknown part in the organization of the human brain," a statement which coincides with the general consensus (Gloor, 1960). Holloway (1966) stresses that the results of these and many other studies of sub-cortical systems indicate the dangers of overemphasizing the role of cortical elaboration in evolution of the primate brain.

8. PLACENTATION

Recent advances in immunochemistry of primates have confirmed some old theories and led to new concepts of taxonomic relationship within the Order (Goodman, 1962a, b, 1963). The progressive improvement of primate placental structure, and thus the increase of intimacy between foetal and maternal circulations, is pivotal to the theory which states that certain proteins such as albumin are stable in an evolutionary sense and can be employed as markers to indicate phylogenetic affinity.

In the formation of the mammalian chorioallantoic placenta, the embryo becomes attached to the uterine wall by means of its outer covering membranes, and it is through this attachment that the embryonic circulation is drawn. The more rapidly this circulation is established and the more intimately the blood systems of the mother and embryo mingle, the more efficient is the nutrition of the developing embryo. The intimacy of the two blood systems, in the terms of Goodman's theory, leads to exchange of proteins, iso-immunization of the mother to the foetal antigens and thus to immunological attack on the foetal proteins by the maternal antibodies which have passed into the foetal circulation.

Two types of placentation in Grosser's classification are found among primates although each type shows a number of variations:

1. Epitheliochorial. In this type, placental formation is diffuse, the outer membrane of the embryo (the chorion) invades the whole of the uterine wall to a limited depth; the maternal and foetal bloodstreams are separated by several epithelial and endothelial layers so that there exists a barrier across which protein exchange is limited. After birth, the placenta is stripped off the uterine wall bringing no maternal layers with it (non-deciduate type). Epitheliochorial placentae are found in Lemuridae and Lorisidae.*

2. Haemochorial. In this form of placentation the chorionic membrane of the embryo becomes intimately attached to a restricted area of the wall of the uterus by an eroding action of the chorionic processes which eventually break through the walls of the maternal blood vessels. In the fully established placenta, the vascular chorionic processes are bathed in crypts of

* According to Gerard (1929, 1931, 1932) the placenta of *Galago demidovii* is of an endotheliochorial type, but see J. P. Hill (1965).

maternal tissue containing maternal blood; thus in this type there are fewer layers to interfere with the free exchange of serum proteins. Haemochorial placentae are found in Tarsiidae among prosimians and in all anthropoid families. The placenta of *Tupaia* which is unique among mammals is said to show certain structural advances towards a haemochorial type (Meister and Davis, 1956, 1958). However J. P. Hill, in a posthumous paper published in 1965, points out that the placenta is unique to primates being of a bidiscoidal, endotheliochorial type.

At one time it was thought that the explanation of placental exchange lay in diffusion and filtration across the foetal and maternal membranes; the rate of diffusion would thus be expected to vary with the number of intervening layers, being greatest in Grosser's type IV, the haemochorial placenta. It now appears (Amoroso, 1959) that placental transfer depends on cytological and cytochemical structure as well as on the disposition of placental blood vessels. Evidence points to an active cellular participation by the placenta.

Goodman's immunological theory, based on the evolution of a haemochorial placenta, is as follows: the process of speciation among higher primates has largely been controlled by acceleration of the rate of variation in the specificity of serum proteins. A protein is composed of polypeptide chains whose component amino-acid sequence is under genetic control: a single gene mutation can produce a change in amino-acid sequence, a change, in other words, in the primary structure of the protein. This means that a new factor is introduced into the "foetal environment" which at this level, may be advantageous or disadvantageous in natural selection. Advantageous mutations in protein synthesis are what Goodman (1963) refers to as "molecular adaptation". The occurrence of a haemochorial placenta, which permits an intimate contact of maternal and foetal circulations and therefore transference of serum proteins, would facilitate maternal iso-immunization against a mutant or variant protein; this would tend to increase the evolutionary stability of proteins such as albumin which are synthesized early in foetal life. This state of affairs does not operate (or rather operates to a lesser extent) in animals which possess the less efficient epitheliochorial placenta since these animals tend—by virtue of the presence of a less "penetrable" placental barrier—to produce greater variation in protein synthesis and thus a greater potential for phenotypic variation.

If Goodman's theory is correct, not only the form of the placenta but also the length of the gestation period adversely affects the survival of mutant proteins by prolonging the period during which immunological attack by maternal antibodies can operate. The effect of prolonged gestation, therefore, would be to slow down the rate of divergence of a given species from its ancestral pattern. The gamma-globulins, serum proteins which appear late in ontogeny, would be less likely to be attacked by maternal antibodies. That these proteins have evolved more rapidly in anthropoid evolution is suggested by the much greater differences in gamma-globulin than in albumin antigenic reactions between anthropoid family groups such as those of the Old and New World monkeys (Goodman, 1962a, b). Goodman postulates that the main phylogenetic lines of advance of the primates were those in which there was an early elaboration of the haemochorial placenta and a marked prolongation of the gestation period. This hypothesis is supported when the fate of the epitheliochorial lemuroid families is compared with that of the haemochorial anthropoid families. Among the lemurs there has been a widely adaptive, but non-progressive, form of evolution; the many terminal products of lemuriform evolution, including the numerous forms now extinct, all have about equal status, fairly low in the grade system of primate phylogeny; this type of evolution is characterized by an early splitting into a number of derived types and is called *cladogenesis*. Anthropoid families on the other hand have shown the type of evolutionary change known



PLATE 5. Skeletons of Primates: a. Marmoset $\times \frac{1}{3}$; b. Baboon $\times \frac{1}{6}$; c. Gibbon $\times \frac{1}{6}$; d. Tarsier $\times \frac{1}{3}$; e. Man $\times \frac{1}{4}$. Scales approximate.

as *anagenesis*, that is to say the anthropoid stock has been characterized by its progressive improvement and *lack* of diversification.

There is no doubt in the minds of primate biologists that the past patterns of prosimian and anthropoid evolution, as judged largely by neontological considerations, were very different indeed. It is still to be proved however whether Goodman's theory, attractive though it is, provides an adequate explanation for this difference in the light of modern theories of protein transference.

New serological data on primates has already led to revision of the taxonomy of the primates, particularly of the Pongidae and their relationship with the Hominidae. The classification of the superfamily Hominoidea into three families: (i) The Hominidae, containing the chimpanzee, gorilla and man; (ii) the Pongidae, containing a monotypic genus, *Pongo*, the orang-utan, and (iii) the Hylobatidae for the gibbon and siamang, is becoming a popular device. It has also led, unhappily, to the grouping of the gorilla and chimpanzee in a single genus, *Pan*, (Simpson, 1963).

9. THE SKULL AND TRUNCAL ERECTNESS

In addition to the list of principal evolutionary trends presented by Clark (1959) and used as a basis for this essay, there are certain progressive adaptations of the primate skull, particularly those relating to posture, which must be referred to. It is clear that the skull reflects in many of its characters the trends already discussed on pp. 6-7. For instance the expansion of the neurocranium, the frontality and isolation of the orbits from the infratemporal fossa, the prognathism of the face and length of the jaws are correlated with evolutionary changes occurring in related systems. The part played by the evolution of the brain, the visual system and the masticatory system of primates in shaping the skull has already been discussed. In addition to the progressive adaptations related to posture, there are certain non-progressive features that nevertheless constitute important differences between members of the primate order; the morphology of the bony ear is of particular importance in this respect (*see* Section 5) and constitutes, with the dentition (Section 6), the principal region of the skull employed in taxonomic judgments.

POSTURAL ADAPTATIONS OF THE SKULL

The foramen magnum of the typical mammalian skull is directed posteriorly while that of primates is directed inferiorly although this is not an absolute distinguishing mark as will be seen. It seems likely that the ventral migration of the foramen magnum is partly an adaptation to the vertical posture of the trunk, which itself can be regarded as a major evolutionary trend of primates, and partly consequent upon the enlargement of the cerebrum (particularly in the occipital region) which has had the effect of "rolling-up" the occiput. The nuchal surface and foramen magnum become progressively displaced from their primitive posterior position to their specialized ventral one as the cerebrum enlarges through the evolutionary grades.

The majority of primates are capable of sitting, clinging or hanging in the vertical position and many of standing and walking with the trunk held vertically (Plate 5). Even in the Tupaiidae, truncal erectness is occasionally seen. Certain prosimian families (Tarsiidae, Indriidae, Lorisidae and Lemuridae) include a number of genera in which a vertical resting posture is

habitual: these genera are grouped in the locomotor category Vertical Clingers and Leapers (see Part III p. 387). They include *Tarsius*, *Indri*, *Propithecus*, *Avahi*, *Lepilemur*, *Galago*, and certain extinct Eocene prosimians such as *Necrolemur*. These forms show a constellation of morphological characters which typify the group, including a projecting occiput, globular brain case and a foramen magnum placed well forward on the base of the skull; in these adaptations, and others relating particularly to the limbs, they are to be distinguished from other genera of these particular prosimian families in which vertical clinging and leaping behaviour is absent, or modified. *Lemur catta*, for instance, though generally regarded as a quadruped, displays in its locomotor behaviour a number of characteristics reminiscent of the Vertical Clinging and Leaping group; *Hapalemur* also probably belongs to this group. In all anthropoid families the erectness of the trunk constitutes at least a part of the postural behavioural repertoire.

Among Cercopithecidae and Hylobatidae, long periods of sitting particularly during night-resting (Washburn, 1957) are facilitated by the presence of specialized pads surmounting the ischium—the ischial callosities (Plate 6). These pads are lacking in Cebidae which usually adopt a horizontal sleeping posture. Ischial callosities show considerable variation between genera. In the more arboreal forms, *Hylobates* and *Cercopithecus* for instance, they are small and well separated; in ground-living members of the Cercopithecinae (e.g. *Papio*, *Mandrillus*) they are large in males and fused across the midline. The discrete or fused nature of the callosities however is not wholly a matter of habitat but rather of taxonomic affinity. The patas monkey (*Erythrocebus*), for instance, while entirely ground-adapted, possesses discrete ischial callosities, a character that underlines its evolutionary relationship to *Cercopithecus*. The mangabeys on the other hand, which are wholly or partly arboreal according to species, possess fused callosities typical of the baboons. This fact, *inter alia*, reflects the close relationship of *Cercocebus* and *Papio* which has sufficiently impressed a number of authorities for them to include both genera (with *Macaca* and *Mandrillus*) in a single subfamily Papioninae (Hill, 1966), or in a separate tribe Cercocebini (Jolly, 1964). The Pongidae and Hominidae sit frequently and also display truncal uprightness and bipedalism in varying degrees. Hominidae are habitually bipedal while Pongidae are only facultatively so. Occasional bipedalism however is not limited to the human and ape families but is observed in Cebidae and Cercopithecidae (Hewes, 1961).

Truncal uprightness is an ancient primate possession as Wood Jones (1916) emphasized in "Arboreal Man"; the fossil tarsiods of the Eocene such as *Necrolemur*, *Nannopithec* and *Hemiacodon* show both cranial and post-cranial adaptations to a saltatory type of locomotion (Clark, 1959; Simons, 1963). The foramen magnum of *Necrolemur* lies almost as far ventrally as it does in modern *Tarsius*. All primates, with one or two exceptions, have a foramen magnum which is directed downwards rather than backwards, although the degree to which it is displaced orally varies considerably. As Schultz has observed (1955), in the foetal and infantile stages of all anthropoid families, the foramen magnum is placed far forward on the ventral aspect of the skull. During the rapid post-natal growth of the face, the foramen gradually shifts backwards. Even in man, some aboral shift occurs (Ashton and Zuckerman, 1956), though the amount of change is less than in anthropoid apes. The aboral shift of the foramen is greater in primates which show marked prognathism than in the short-faced forms; among the Cebidae, the short-faced squirrel monkey (*Saimiri*) for instance possesses a foramen sited almost as far forward as it is in man, while in the markedly prognathic *Pongo* and *Gorilla* the foramen is directed as much posteriorly as it is ventrally. Only in the howler monkey (*Alouatta*) among the Cebidae does the foramen magnum occupy a near-

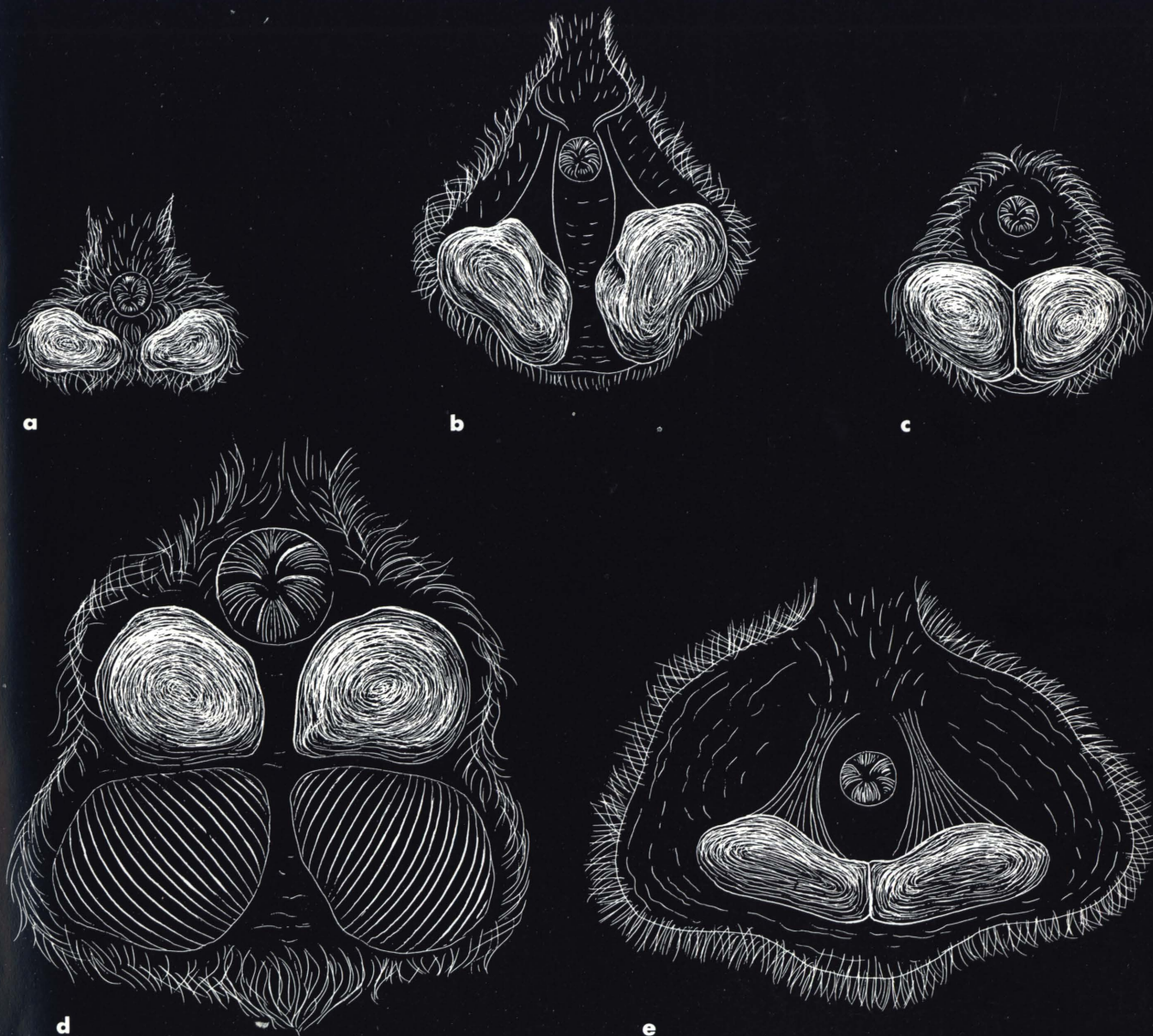


PLATE 6. Ischial callosities of primates: a. ♂ Mona monkey; b. ♂ Pigtailed Macaque; c. ♂ Barbary ape; d. ♂ Gelada baboon; e. ♂ Guinea baboon.

mammalian position; this character is associated in howlers with other remarkable modifications of skull topography, which are generally regarded as expressions of the highly specialized nature of the vocal apparatus in this genus.

In man the forward position of the foramen magnum and thus of the occipital condyles allows the head to be balanced on the top of the vertebral column without the need of a powerful set of neck muscles to offset the weight of the face and jaws; but in *Gorilla*, for instance, the face and jaws are so heavy, and the pivot so far back, that extremely strong muscles are required at the back of the neck to provide a counterbalancing force. In *Gorilla*

and other genera such as *Pongo*, *Papio* and *Mandrillus* in which this imbalance operates, the nuchal area of the skull is enormously expanded to provide an additional area of attachment for the bulky posterior neck muscles; in *Gorilla* and *Pongo* a raised flange, the nuchal crest, which is a functional analogue of the sagittal crest, is usually present in the adult males (Ashton and Zuckerman, 1956). The functional relationship between the sagittal and nuchal crests in primates has been the subject of considerable controversy particularly with respect to the occurrence of such crests in the Australopithecinae (Robinson, 1958). Nuchal and sagittal crests owe their formation to two distinct biomechanical forces, the one concerned with posture and the other with jaw size. In certain forms the two forces operate with equal intensity. Therefore nuchal crests may develop in the absence of sagittal crests as in *Colobus polykomos*, (Vogel, 1962), or sagittal crests may develop in the absence of nuchal crests as in *Nycticebus coucang* (Seth, 1964) and *Colobus verus* (Vogel, *loc. cit.*), or sagittal and nuchal crests may develop together in confluence, as in *Gorilla* and *Pongo*.

In conclusion it would seem that the displacement ventrally and orally of the foramen magnum and occipital condyles is primarily an adaptation for truncal erectness and is an evolutionary trend of primates. It would also seem that the conflicting demands of the masticatory apparatus have led, secondarily, to an aboral migration of the foramen in certain long-faced and heavy-jawed forms.

10. GROWTH RATES AND THEIR EFFECTS

The structural characters of an adult primate are ultimately dependent on the genetical constituents of the zygote nucleus. Some characters appear in early foetal life, some are present at birth, some appear during early post-natal life, in others development is delayed until adult life; certain characters are directly related to the primary gene product, others are the result of interactions during ontogeny of environmental factors such as diet, climate and so on.

Embryonic and foetal development and post-natal growth, though frequently presented to the student as discrete and separate events, are a continuous process; and it is not until the fully adult stage is reached that the "final product" is ripe for taxonomic assessment in the totality of its characters. Even then, as Schultz (1956) has pointed out, ontogeny is by no means over. Although it is probably legitimate to regard such later changes as occur, as degenerative, they are still species-specific and therefore of phylogenetic significance. Characters of sub-adult, even infant, primates *can* however be used intraspecifically in taxonomic practice and in palaeontology, provided they are compared with other specimens of comparable developmental age; interspecific comparisons are more dangerous for as Schultz (1963) points out: "... every single feature can independently shift its place in the sequence of ontogenetic processes in either direction" (p. 89). As an example of this, the fusion of the *os centrale* of the carpus may be quoted; the fusion of this bone to the neighbouring scaphoid (navicular) occurs early in the pre-natal stage of ontogeny in man, soon after birth in the great apes and in late adult life in gibbons and some monkeys. The fusion of the *os centrale* in man, viewed in this perspective, loses its unique "qualitative" nature and becomes a non-specific quantitative character. Absence of an *os centrale* is, none-the-less, a character of taxonomic significance in man, but only in the *time* of its disappearance as a separate entity and not in the fact of its fusion. The early fusion of the *os centrale* in man is an example of acceleration of the growth process. Other accelerations in man (relative to non-human primates) are the early

descent of the testes, the fusion of the sternbrae, the early closure of the premaxillary suture and the early development of a mastoid process. Retardations or "foetalisations" as they were termed in Bolk's (1926) theory, are an important source of human specializations but, as is now clearly appreciated, not the only source. Alterations in growth rates that are generally regarded as retardations (Schultz, 1950) include the retention of the foetal position of the head on the vertebral column, lack of forward growth of the orbits and of the face, and lack of rotation of the great toe. Many of these growth modifications such as the position of the head on the vertebral column and the lack of rotation of the big toe are foetal "retentions" rather than foetal retardations. Little if any change occurs in the foetal position of the head in modern man throughout ontogeny. Modern man has "foetalized" as far as he can go by retaining precisely the foetal condition.

Reduction, that is to say the disappearance of structures, is a relatively rare phenomenon but when it occurs, it is liable to be regarded as a qualitative distinction; in fact, as Schultz has shown, reduction is merely the extreme expression of the retardation mechanism and is therefore essentially quantitative. Such reductions in man include the disappearance of the *os penis*, an apparently unique human character. The fact that man's closest simian relative, the gorilla, possesses an *os penis*, albeit very small, while man has no trace of such a structure, is on the face of it, a major distinction. From the lemurs to anthropoid apes, a relative reduction in size of the *os penis* is apparent; but from gorilla to man there is, apparently, to use Simpson's term, a quantum jump. The final reduction in man of the *os penis* is the culmination of an evolutionary trend, as Schultz has shown, characterizing the primates. Like so many qualitative distinctions that in the past have been proposed for man and found, on further study, to be merely quantitative, the disappearance of the *os penis* will, no doubt, be demonstrated as a continuous and gradual process when the fossil record of early hominids is more complete. The disappearance of the shaft of the pisiform in man is another example.

Accelerations, retardations, retentions and reductions are some of the mechanisms by which innovations in the genotype are reflected in the specificity of the phenotype; these processes act by modifying the differential growth velocities and new phenotypes—new species—may then evolve. Normally regulatory forces, which have a genetic basis, hold the growth processes involved in ontogeny in pre-determined channels. Tanner (1962) has demonstrated the action of these forces by plotting maturity gradients in various parts of the human body. Maturity gradients in the lower limb, for instance, show that at all ages of development the length of the foot is nearer its adult status than the length of the leg below the knee; and that this segment is similarly nearer the adult status than the thigh segment. The maturity gradient is thus from the foot to the thigh. In the individual, disturbances of the regulatory forces lead to developmental abnormalities; in populations, subject to natural selection, disturbances in differential growth rates may, if beneficial, lead to new adaptations. Reference in this discussion principally has been made to man, but it should be clear that the same processes operate for all non-human primates; if man, however incorrectly, can be called a "neotenuous ape", *Cercopithecus* monkeys can be described as "neotenuous baboons".

Tanner (1962) has shown that the characteristic shape of human weight growth curves is shared with chimpanzees and rhesus monkeys. There is no reason to doubt that other Old World monkeys and apes, indeed other primates, show similar curves; it is merely that growth studies have been limited so far to these two forms. Gavan and Swindler in a recent paper (1966) point out that the similarity in shape of growth rate among chimpanzees, rhesus monkeys and human infants, is not due so much to a basic primate growth curve as to a basic mammalian one.

A trend to prolong post-natal life is apparent in the primates. The data, which are far from complete or certain, are presented in Table II and indicate that the normal life span has become extended from 14 years in the prosimians to 75 years in modern man. In past human populations, however, the average expectancy of life was considerably lower than 75 years; such figures include deaths in infancy and deaths from plagues and warfare, so that they constitute more of a social index of life expectancy than a biological one; there is no evidence for instance, that in past populations, the juvenile phase was of shorter duration than it is now. The period which shows the least change between the apes and man is the foetal phase or gestation period; whereas the duration of infantile, juvenile and adult phases has doubled, the intra-uterine phase has remained the same. In some respects man's intra-uterine development is accelerated but in most features such as ossification, brain size and myelination of peripheral nerves, his development is clearly retarded compared with that of other primates. Man produces absolutely and relatively the largest infant at birth of all primates, but the ossification

TABLE II

Duration of Life Periods

	<i>Foetal phase</i> (days)	<i>Infantile phase</i> (years)	<i>Juvenile phase</i> (years)	<i>Adult phase</i> (years)	<i>Life span</i> (years)
Lemur	126	?	?2	11 +	14
Macaque	168	1½	6	20	27-28
Gibbon	210	?2	6½	20 +	30 +
Orang-utan	233	3½	7	20 +	30 +
Chimpanzee	238	3	7	30	40
Gorilla	265	3 +	7 +	25	?35
Modern Man	266	6	14	50 +	70-75

Table shows duration of life periods of primates derived from many sources. Foetal phase is equivalent to gestation period. Life span is the summation of the three post-natal phases. Uncertainty is indicated by ? or a + sign.

of the bones of the hand lags far behind that of macaques, and somewhat behind that of chimpanzees.

At birth the human infant's brain is 25% of its adult size compared with the 70% of the brains of macaques and gibbons. Thereafter the brain grows rapidly in man, the maximum growth period being in the first three years; at the end of this time the brain is 75% of its adult size having an average cranial capacity of 1225 cc. Thereafter the infantile brain "spurt" subsides and further growth occurs *pro rata* with the growth of the body. Similar "spurts" in body weight growth occur in non-human primates but start earlier in the post-natal period and are of shorter duration. The retardation and prolongation of the brain-growth period in humans reflects the complexity of the neuronal organization and connections in the adult.

The absolute size of the human brain at birth, which weighs on average 350 g, can be correlated with the fact that the human gestation period has not become extended as have all his other life periods. Prolongation of the intra-uterine phase by, for example, three months, would mean that the brain would weigh approximately 526 g. The size of the infant's head would then be incompatible with the size of the birth canal. The gestation period is terminated in man (and other primates) when the size of the head is consonant with a safe delivery.

Selection for increased pelvic dimensions in man would seem a possible way in which nature could meet this critical situation, but the pelvic dimensions are fixed by the demands of upright bipedal walking. Thus two evolutionary trends, the increased size of the human brain and the adaptations of the pelvis consonant with bipedalism, are at variance. The solution, as in the case of most adaptations, is an evolutionary compromise.

Tanner (1962) points out that the essential change between higher primates (monkeys and apes) and mammals is the postponement of menarche in the females and puberty in the males until growth is nearly complete. In the rhesus monkey (*M. mulatta*) as in man, the adolescent growth spurt precedes the onset of puberty in males (Fig. 3). The magnitude of the difference between the male and female adolescent spurts reflects, in part, the degree of sexual dimorphism in the adults.

Tanner (1962) regards the existence of an adolescent spurt as an evolutionary trend of primates. The postponement of puberty until growth is nearing completion may be advantageous for the evolution of social life among the higher primates. Postponement of puberty ensures a tractable, non-sexually competitive group of juveniles within a band or troop. Such

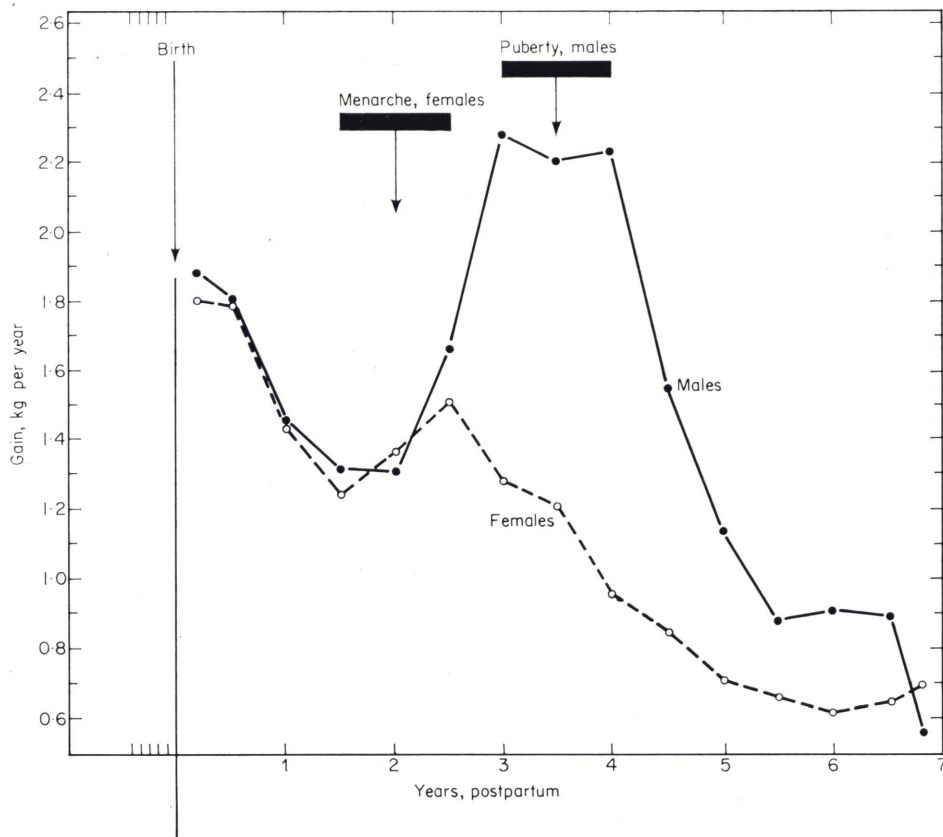


FIG. 3. Weight velocity curves for the rhesus monkey. Curves resemble those of man and show the adolescent spurt in males and females. [From J. M. Tanner (1962), "Growth at Adolescence", 2nd Ed. Blackwell, Oxford.]

an arrangement has obvious advantages in a baboon troop for instance where group-survival is in the hands of a few dominant and fully adult males; the presence of hordes of sexually

mature, though physically immature juveniles, would lead to intragroup aggression and fighting, a feature which is so markedly lacking in free-ranging baboon troops.

The trend for prolongation of life periods in the primates is closely related to the increasing importance of learned behaviour in the Order. The period of immaturity is a period of dependency and during this time the infant primate is learning, through his mother and other members of the group, the *mores* of his complex social life.

PART II

Profiles of Primate Genera

Index to Profiles

Profiles are arranged alphabetically according to generic name. The common name equivalents of each genus are listed below in alphabetical order.

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Baboon	<i>Papio</i>	p. 247-257
Barbary Ape	<i>Macaca</i>	p. 207-219
Bearded Saki	<i>Chiropotes</i>	p. 120-122
Bushbaby	<i>Galago</i>	p. 148-159
Capuchin monkey	<i>Cebus</i>	p. 87-93
Celebes Black Ape	<i>Cynopithecus</i>	p. 132-136
Chimpanzee	<i>Pan</i>	p. 238-246
Douc Langur	<i>Pygathrix</i>	p. 293-294
Douroucoulis	<i>Aotus</i>	p. 53-55
Drill	<i>Mandrillus</i>	p. 220-223
Dwarf Lemur	<i>Cheirogaleus</i>	p. 117-119
Feather-tailed Treeshrew	<i>Ptilocercus</i>	p. 289-292
Fork-marked dwarf lemur	<i>Phaner</i>	p. 262-263
Galago	<i>Galago</i>	p. 148-159
Gelada	<i>Theropithecus</i>	p. 326-329
Gentle Lemur	<i>Haplemur</i>	p. 168-171
Gibbon	<i>Hylobates</i>	p. 172-178
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Golden Lion Marmoset	<i>Leontideus</i>	p. 197-199
Gorilla	<i>Gorilla</i>	p. 160-167
Guenon	<i>Cercopithecus</i>	p. 100-116
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Langur	<i>Presbytis</i>	p. 274-283
Leaf-monkey	<i>Presbytis</i>	p. 274-283
Lemur	<i>Lemur</i>	p. 188-196
Loris	<i>Loris</i>	p. 203-206
Macaque	<i>Macaca</i>	p. 207-219
Madras Treeshrew	<i>Anathana</i>	p. 52
Mandrill	<i>Mandrillus</i>	p. 220-223
Mangabey	<i>Cercocebus</i>	p. 94-99
Marmoset	<i>Callithrix</i>	p. 79-83
Mouse lemur	<i>Microcebus</i>	p. 224-227
Night monkey	<i>Aotus</i>	p. 53-55
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COMMON NAME	GENERIC NAME	
Pagai Island Langur	<i>Simias</i>	p. 314-315
Patas monkey	<i>Erythrocebus</i>	p. 143-147
Pentailed Treeshrew	<i>Ptilocercus</i>	p. 289-292
Philippine Treeshrew	<i>Urogale</i>	p. 337-339
Pinché	<i>Saguinus</i>	p. 299-308
Potto	<i>Perodicticus</i>	p. 258-261
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Snub-nosed Langur	<i>Rhinopithecus</i>	p. 295-298
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Tamarin	<i>Saguinus</i>	p. 299-308
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Woolly monkey	<i>Lagothrix</i>	p. 182-187
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Use of asterisk in Profiles denotes data based on very limited or even single observations. Small numbers used in text indicate authorities who are listed in numerical order at the end of each profile.

ALOUATTA† Lacépède, 1799

Howlers

5 species: 21 subspecies^{1, 2, 3, 11}

<i>A. villosa</i> [= <i>A. palliata</i>]	Mantled Howler	8 subsp.
<i>A. seniculus</i>	Red Howler	5 subsp.
<i>A. belzebul</i> (Type species)	Red-handed Howler	5 subsp.
<i>A. fusca</i> [= <i>A. guariba</i>]	Brown Howler	3 subsp.
<i>A. caraya</i>	Black Howler	0 subsp.

GEOGRAPHICAL RANGE^{2, 4}

Central and South America. *Alouatta* are found from sea level to 6560 ft. (2000 m) in altitude. *A. villosa* found in coastal forests of Mexico, throughout central America (save Yucatan) and in Pacific coastal forests of S. America as far as 3° S. Remaining species are found throughout forested areas of S. America; *A. caraya* extends into the Gran Chaco. Also found in mountains of the S.E. littoral of Brazil (*A. fusca*).

ECOLOGY

HABITAT:⁵ Tropical rain forest and mixed deciduous forest. Upper and middle canopy of forest preferred; generally avoid secondary growth. Feed in the smaller branches of emergent trees. ACTIVITY RHYTHM: Diurnal. DIET:⁶ Predominantly a leaf-eater; also buds, flowers and fruit, particularly figs [see Carpenter (1934) for list of food plants of *A. villosa*].

MORPHOLOGY

External Characters

Large, robust prehensile-tailed monkeys with long fur, black in *A. villosa*, brown in *A. fusca*, copper-red in *A. seniculus*, and black with reddish hands, feet and tailtip in *A. belzebul*. Sexual dichromatism in *A. caraya*: ♂ black, ♀ and juvenile olive-buff.⁷ In all species, face is bare and deeply pigmented. Nostrils close together.⁸ Swelling beneath the chin, accommodating the specialized larynx, is outlined by a beard in the ♂; it is much more prominent in the ♂ than in the ♀. The head is set low on the shoulders giving a hunched appearance. The tail is very mobile; the distal quarter of the underside bears naked skin with papillary ridges. Arms and legs subequal. Big toe divergent and opposable. HAND: Digital formula: 3.4.2.5.1. or 3=4.2.5.1. Genitalia of both sexes are prominent. MAMMAE: 2 nipples situated near the axilla.⁴

Weights and Dimensions^{3, 4, 16, 9}

	♂	♀	♀ in % ♂
Average weight (g)	7392 (4♂♂)	5720 (4♀♀)	77
Head and body length range (mm)	465-720 (35♂♂)	390-573 (34♀♀)	81
Tail length range (mm)	490-748 (35♂♂)	490-711 (34♀♀)	93

Considerable sexual dimorphism in weight, e.g. Schultz (1956) gives ♀ in % of ♂ = 81% (198 specimens). Dimorphism less marked in tail length.

† See Taxonomic Notes, p. 370.

GORILLA† I. Geoffroy, 1852

Gorillas

1 species: 3 subspecies^{1, 2}

<i>Gorilla gorilla gorilla</i> (Savage and Wyman, 1847)	Western Lowland Gorilla
<i>Gorilla gorilla beringei</i>	Eastern Highland Gorilla
<i>Gorilla gorilla manyema</i>	Eastern Lowland Gorilla

GEOGRAPHICAL RANGE^{2, 3, 4}

Equatorial Africa: a discontinuous distribution. The western gorilla range extends from the extreme S.E. of Nigeria (Cross River district) through Cameroun, Spanish Guinea,⁴⁸ Gabon, Congo (Brazzaville) and the Central African Republic, south to the mouth of the R. Congo and east to the valley of its tributary, the R. Sangha.

The eastern gorilla is widely scattered in isolated population units over an area of 35,000 sq miles: *G.g. manyema* from the lowlands east of the Upper Congo (Lualaba) R. to the mountains west of L. Edward and west of the northern tip of L. Tanganyika; *G.g. beringei* in the Virunga Volcanoes and Mt. Kahuzi district, the high mountains to the north and east of L. Kivu. There are also gorillas in the Kayonza forest of S.W. Uganda: these probably belong to *G.g. manyema*. *Latitudinal range*: 0°–4° 20' S. (eastern), 6° N.–5° 30' S. (western). *Longitudinal range*: 26° 30' E.–29° 45' E. (eastern), 9° 30' E.–17° 60' E. (western).

ECOLOGY

HABITAT:^{3, 5} Lowland rain forest and montane rain forest up to 8000 ft (2438 m), also bamboo forest up to 10,000 ft (3048 m). In the Virunga Volcanoes area gorillas are found in *Hagenia* woodland where trees are low and there is a dense herbaceous understorey, and also on the open slopes above, up to an altitude of 13,500 ft (4115 m). Gorillas have been seen 50 m below summit of Mt. Muhavura (4127 m).⁶ Life is largely (90%) spent on the ground during the day;^{6, 7} brief forays into trees by both sexes but principally by ♀♀ and juveniles. **DIET**:^{3, 5, 6, 7} wholly vegetarian. Lowland gorillas are said to eat some fruit^{8*} but highland gorillas apparently eat little. Principal items of diet of highland gorillas are bulk foods and include pith, stalks, vines, bark, leaves, bamboo shoots and roots. Donisthorpe (1958), Schaller (1963, 1965) and Kawai and Mizuhara (1959) supply lists of food items. Lowland gorillas raid native plantations of bananas and sugar cane.^{8*} **ACTIVITY RHYTHM**: Diurnal. **PREDATORS**: Leopards,* Man. Merfield (1956) and Donisthorpe (1958) report fear of dogs.

MORPHOLOGY

External Characters

Mature ♂♂ commonly reach 6 ft in bipedal standing height, weigh 300–400 lb and have an arm span of well over 8 ft. Mature ♀♀ are approximately half the weight of the males.

The face is bare and jetblack in colour, the nostrils are flared and surrounded by prominent alar folds; the appearance of the nose has been likened to a “squashed tomato”. The eyes are wide-set and deeply sunk under prominent supra-orbital ridges; the ears are small and set flat against the head. The head is conically elongated in adult ♂♂ due to the prominent nuchal and sagittal crests surmounting the skull. The arms are long (particularly in the lowland forms)

† See Taxonomic Notes, p. 373.

and the hands broad. The thumb is relatively shorter than man's and is less well muscled. The legs are short and outwardly rotated at the hip; the foot is plantigrade and the heel long. In the western gorilla the big toe is stout, short and well abducted; in the eastern highland form it is proportionately somewhat longer and is less abducted;⁹ the remaining toes are syndactylous, markedly so in the eastern gorilla.

Coat and skin colour in all races is black or blackish. The western form may show a brownish or russet colouration to the crown of the head;¹⁰ the eastern form is usually jet-black all over with occasional white streak between ears. Mature males of all three races show a saddle of white or silvery hair across the lumbar region, most pronounced in Eastern race (*G.g. beringei*). Adults of *G.g. beringei* may have only a grey spinal stripe⁷ (? young ♂♂). Hair of coat is short, dense, bristly and coarse in lowland gorilla but longer and thicker, especially on the arms and forearms, in the eastern highland form. The face and upper part of the chest are bare. Western gorilla has a distinct "lip" to the nose overhanging the septum, which is absent in the Eastern races. (See Plates 46, 47.)

Weights and Dimensions

BODY WEIGHT RANGE: In the wild: ♂ 140–180 kg (300–400 lb); ♀ 75–110 kg (165–240 lb). In captivity, body weight may be as much as 636 lb for a ♂ eastern gorilla ("Ngagi", San Diego Zoo) and 578 lb for a ♂ western gorilla ("Bobby", Berlin Zoo).¹¹ "Guy", a western form, living in the London Zoo, at present weighs over 450 lb. Heaviest ♀ weight: "Oka" of Bronx Zoo weighed 280 lb when 13 years old.

External Measurements ♂ Gorilla²

Race	Weight	Height	Girth	Arm-span	Arm Length	Leg Length	Foot Length
<i>G.g. gorilla</i>	307.3(6)	168.5(25)	143 (19)	233.7(17)	111.6(8)	76.8(8)	28.8(9)
<i>G.g. manyema</i>	360.3(2)	175 (4)	152.3(3)	259.5(2)	114.0(2)	79.0(2)	32.5(1)
<i>G.g. beringei</i>	342.9(13)	172.5(6)	146.7(13)	227.5(10)	106.0(4)	76.3(3)	29.7(11)

Linear measurements in centimetres; weight in pounds.

Internal Characters

For detailed anatomical studies see Keith (1896), Duckworth (1915), Sonntag (1924), Schultz (1927), Raven (1950), Steiner (1954). For structural differences between *G.g. gorilla* and *G.g. beringei*, see Schultz (1934). The following characters are selected principally on the basis of their known functional importance or for their value for identification. **SKULL:** Neurocranium, facial skeleton large. Cranial capacity 340–685 cc in adult ♂;¹² largest cranial capacity recorded 752 cc.¹³ Calvarium surmounted by large bony flanges; in nearly all adult ♂♂ there is a sagittal crest and, in all, a nuchal crest is present. ♀♀ show some creasing in 30%. Mastoid process is very variable in size; sometimes large and sometimes absent; this process continues to grow throughout adult life.¹⁴ Face is markedly prognathic; orbits are rectangular and widely separated by fused nasal bones which are pinched up to form a sharp median crest; supra-orbital ridge strongly developed and deeply excavated by frontal air sinus.¹³ Hard



palate is very long and extends well beyond 3rd molar, particularly in *G.g. beringei*.¹ Mandible is very stout and lacks a "chin"; the R and L halves of the mandible are braced by a shelf of bone, so-called "simian" shelf. VERTEBRAL COLUMN: 3rd to 7th cervical spines long, very stout and non-bifid; Thoracic vertebrae: 13, Lumbar vertebrae: 3-4 (commonly 17 thoracolumbar vertebrae in lowland form and 16 in highland form).¹⁵ Sacral vertebrae: 5-6. STERNUM: broad but elements remain separate (cf. *Pan*). SCAPULA: Sinuous vertebral border in *G.g. beringei*—straight border in other two races. HAND: os centrale fused with scaphoid. Phalanges stout, heavily buttressed and only slightly curved. Skin on back of middle phalanges is typically modified to form knuckle pads.^{16, 17} FOOT: tarsus length and heel length are greater than in any primate except man.¹⁸ DENTITION: D.F. = $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} = 32$. Dental characters are very like *Pan*: in *Gorilla* however the molar cusps are sharply defined and "crystalline" in appearance and the lower molar series increases in size from M_1 to M_3 ; in upper jaw M^3 is often slightly smaller than M^2 . Supernumerary molars occasionally present (4%) but supernumerary premolars very rare (see Schultz, 1964). ALIMENTARY SYSTEM:^{19, 20, 21} caecum and colon very large. Appendix present. Liver lobes variable in number, up to 6 lobes reported. VASCULAR SYSTEM: coronary vessels (see Hall-Craggs, 1961). THORACIC VISCERA (see Washburn, 1950). GENITO-URINARY SYSTEM (see Steiner, 1954 and Koch, 1937). LARYNX: laryngeal air-sacs present.

Genetic Biology

CHROMOSOMES:²⁴ *G. g. gorilla* $2n=48$ (1♂, 2♀). IMMUNO-CHEMISTRY: See the studies of Goodman (1962, 1963a and b, 1964), Williams *et al.* (1961) and Williams (1964). Serum precipitin data demonstrates close phyletic affinity of *Gorilla*, *Pan* and *Homo*. HAEMOGLOBINS: Human and gorilla Hbs differ insignificantly in amino-acid composition. P.T.C. TASTING:³¹ tasters: non-tasters as 14: 4. BLOOD GROUPS: *Gorilla* shows ABO polymorphism, although "O" phenotype is lacking (Franks, 1963). See also Wiener *et al.* (1966).

BEHAVIOUR

Locomotor Behaviour

AUTHORS' CLASSIFICATION: Brachiation. Subtype: Modified Brachiation. When on the ground the gait is quadrupedal, the weight of the body being taken on the plantigrade feet and the backs of the middle phalanges of the fingers. Bipedal locomotion rare in the wild.³ Erect standing occurs during chest-beating display. True brachiation (see Part III, p. 388) never seen in adults or juveniles. Tree-climbing more common in infants and ♀♀ than in ♂♂ and is particularly common in Kayonza gorillas according to Pitman (1935) where night-nests are built high in trees. LIMB PROPORTIONS: For Indices, see Part III, p. 394.

Hand Function

Hand prehensile, thumb opposable. Hands are used extensively in plucking and manipulating food objects and in nest-building. No evidence of tool-using or tool-making.^{3, 7} Thumb plays a relatively larger role in manipulation than in chimpanzees but less than in man. HAND PROPORTIONS: see Part III, p. 401.

Resting Posture

Gorillas make ground- or tree-nests of simple construction; nests are never used two nights consecutively. Siting of nests is clearly related to habitat;^{3, 7, 33} in *Hagenia* woodland 97% nests are on ground; in eastern lowland rain forest only 22% are on the ground, these being nests of silverback males. Day-nesting⁵ apparently more common among eastern than western gorillas.^{33, 34} Eastern gorillas invariably foul their nests during the night.

Social Behaviour

A number of field studies of Eastern highland gorillas have been carried out since 1921, notably by Akeley (1922), Coolidge (1929), Bingham (1932), Pitman (1935), Donisthorpe (1958), Kawai and Mizuhara (1959), Emlen and Schaller (1960), Osborn (1963), and Schaller (1963, 1965). Western gorillas have not been extensively studied. For captivity studies, see principally Yerkes and Yerkes (1929).

The following account is derived principally from the field work of Schaller (1963, 1965) and relates to *G.g. beringei* unless otherwise stated. **GROUP STRUCTURE:** Eastern gorillas live in groups consisting of between 5 and 30 members; average size of groups varies from region to region. Groups are cohesive and relatively stable. Change in group composition limited to birth of infants, and comings and goings of individual adult males. **GROUP COMPOSITION:** Adult sex ratio: 1♂ : 2♀♀. Each group contains at least one silverback ♂, one or more black-back ♂♂, several ♀♀, juveniles and infants. This composition holds true also for western gorillas.⁸ Lone ♂♂, usually young adults, are quite common, briefly attaching themselves to existing groups [see also Merfield and Miller (1956); Kawai and Mizuhara (1959)].

Intra-group Behaviour

Generally peaceful. **DOMINANCE:** Group activity determined by dominant ♂ who acts as leader and protector; there is little overt dominance activity. Among subordinate ♂♂ there is some evidence of a linear hierarchy; among ♀♀, hierarchy may relate to infant-carrying; among juveniles, it appears to be based on size. **GROOMING:** Infrequent and never reciprocal; principally seen between mother and infant. Grooming appears to have a low social valency. **COMMUNICATION:** by means of posture, facial expression and vocalization. Vocalization is agreed by all observers to be unobtrusive. Schaller has listed 21 distinct sounds. **PLAY:** Infants play frequently on their own or in juvenile-infant play groups, but play is not obtrusive. **CHEST-BEATING DISPLAY:** Ritualized sequence of 9 discrete acts culminating in chest-beating with cupped hands. Excitement producing a build-up of tension is stimulus to display, and its function is probably intimidation. **HOME RANGE AND TERRITORIALITY:** 10–15 sq miles. Group ranges may overlap but there is no aggression or "defence" of territory. Daily range is very small and seldom exceeds 1 mile although Donisthorpe's (1958) study indicates somewhat greater distances on occasions in Virunga Volcanoes area. **POPULATION DENSITY:** Variable. Highest density in Virunga Volcanoes area: 6.6 per sq mile.

Sexual Behaviour*

Copulation seen only twice in 12-month study period in the wild. In captivity, among western gorillas, copulation is both *more canum* and *more hominum*.^{38*}

REPRODUCTION AND DEVELOPMENT

Field evidence does not indicate any fixed breeding season.³ **SEXUAL CYCLE:*** in captivity lasts for 30–31 days; periodic genital swelling is present (Raven, 1936) and menstrual bleeding is minimal. **GESTATION PERIOD:*** 251–289 days (records from 5 captive births).

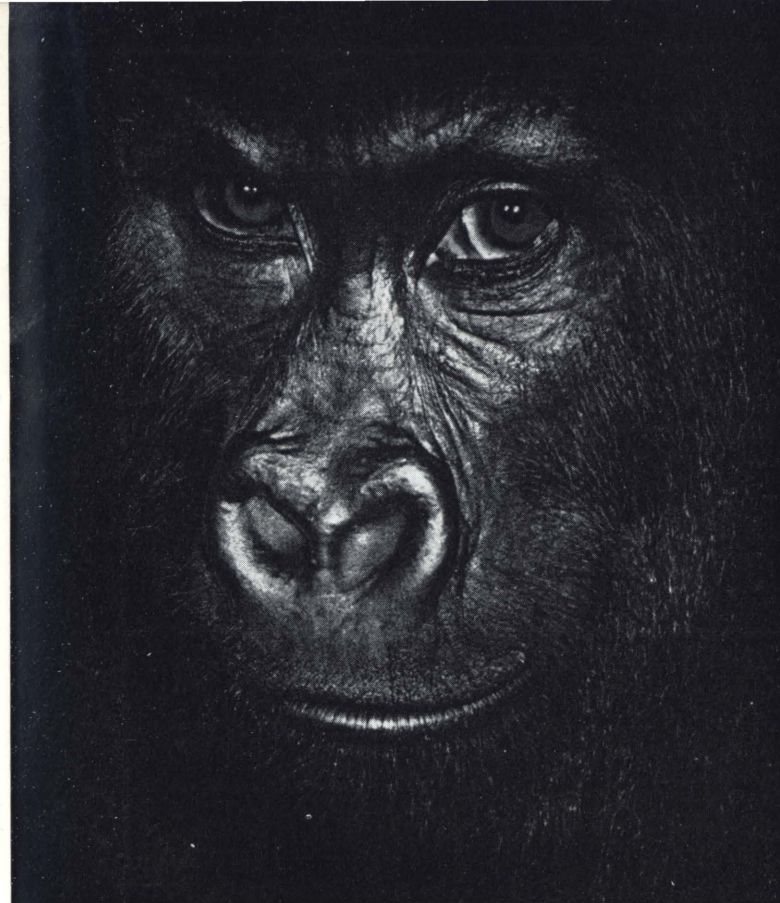
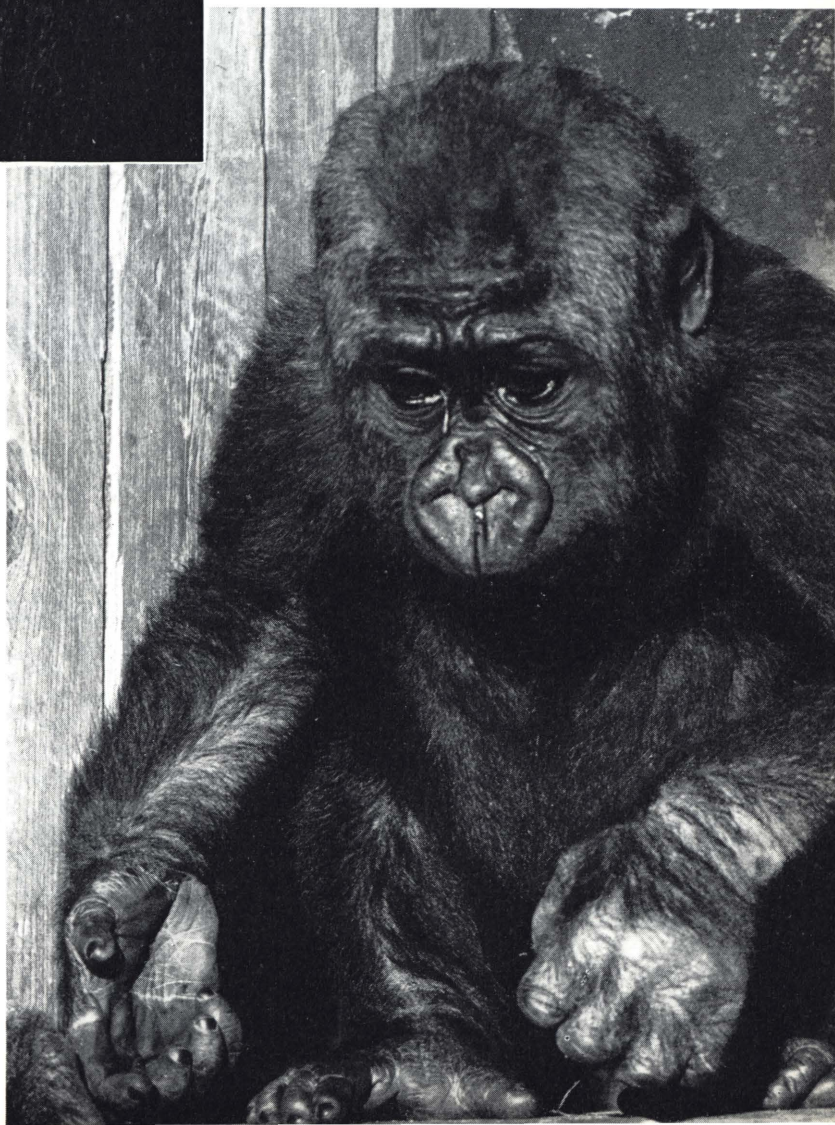


PLATE 47. Above: Eastern Highland Gorilla, *Gorilla gorilla beringei* (Eric Kirkland); below: *Gorilla gorilla gorilla*, young ♂ aged 2 years (by courtesy of Doris M. Sorby)



LABOUR: Unrecorded in detail, but *see* Lang (1962). INFANT DEVELOPMENT:* In the wild,³ infant remains with mother for first 3 years, being partly weaned by 1 year. At 1/12 infant can hold on to mother; at 3/12 it rides prone on her back and at 6-7/12 infants are walking and climbing unaided. For the development of the captive infant, *see* Lang (1960, 1962), Carmichael, Kraus and Reed (1962), Rumbaugh (1965c).

CAPTIVITY

LONGEVITY: (in wild)* 25-30 years. LONGEVITY RECORD:⁴² Western Lowland Gorilla: 33 years 5 months, Philadelphia Zoo. BIRTHS IN CAPTIVITY:⁴³ to date, 8 births (*G.g. gorilla*) have taken place in captivity. Only recorded case of twins: Frankfurt, May 1967 to Makulla. Birth Weights, 1.7 kg and 1.8 kg.

Zoo	Date	Name and sex	Parent	Parent	Weight at birth (kg)
Columbus Zoo U.S.A.	Dec. 22nd 1956	Colo ♀	The Baron	Christina	1.87
Basle Zoo Switzerland	Sept. 23rd 1958	Goma ♀	Stephi	Achilla	1.82
Basle Zoo Switzerland	April 17th 1961	Jambo ♂	Stephi	Achilla	2.7 (9 weeks)
National Zoo Washington	Sept. 9th 1961	Tomako ♂	Nikumba	Moka	2.27
National Zoo Washington	Jan. 10th 1964	Leonard ♂	Nikumba	Moka	Not weighed
Basle Zoo Switzerland	June 1st 1964	Migger ♂	Stephi	Achilla	3.95 (11 weeks)
San Diego Zoo U.S.A.	June 3rd 1965	Alvila ♀	Albert	Vila	2.14
Frankfurt Zoo W. Germany	June 22nd 1965	Max ♂	Abraham	Makulla	2.1

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PLATE 48. *Gorilla gorilla beringei*; Above: growth series of male skulls from infant (L.) to adult (R.). (Naturhistoriska Riksmuseet, Stockholm). Below: hand of young ♂.

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HYLOBATES† Illiger, 1811

Gibbons

6 species: 15 subspecies^{1, 2, 3, 4, 5, 6, 7}

<i>H. lar</i> (Type species)	White-handed gibbon	3 subsp.
<i>H. agilis</i>	Dark-handed gibbon	0 subsp.
<i>H. moloch</i>	Silvery gibbon	6 subsp.
<i>H. hoolock</i>	Hoolock gibbon	0 subsp.
<i>H. concolor</i>	Black gibbon	6 subsp.
<i>H. klossii</i>	Kloss's gibbon	0 subsp.

GEOGRAPHICAL RANGE^{5, 8}

Southeast Asia. Gibbons are confined to areas of primary forest. *H. lar* is found in Indo-China and Thailand to the west of the R. Mekong, in Tenasserim, the Malay peninsula and Sumatra. *H. hoolock* is found in Assam, Burma and West Yunnan; *H. concolor* in Vietnam and Laos, E. of the R. Mekong, and Hainan island. *H. agilis* is sympatric with *H. lar* in Malaya and Sumatra; *H. moloch* is the only species found in Java and Borneo. *H. klossii* is confined to the Mentawai islands, off the W. coast of Sumatra. Limits of genus: 29° N.–9° S. 90–120° E.

ECOLOGY

HABITAT:⁹ Arboreal. Tropical rain forest, semi-deciduous forest and montane forest up to about 2000 m. Gibbons prefer the closed canopy but during feeding they may climb to the highest emergent crowns or descend to clumps of bamboo and low bushes; or to the ground to drink. Do not build nests, but sleep amongst dense foliage. **ACTIVITY RHYTHM:** Diurnal. **DIET:**⁹ 80% fruit, 20% leaves, buds and flowers; sometimes birds' eggs, young birds and insects. Fluid largely acquired from fruit but also obtained from licking bark and leaves after rain; occasionally drink from springs.

MORPHOLOGY

External Characters^{1, 5}

Hylobates are small tailless apes with long dense shaggy fur varying from black or dark brown to pale fawn or silver grey. Face is bare and deeply pigmented, as are the palms and soles. Arms and hands are extraordinarily elongated, legs and feet less so. Moderate-sized ischial callosities are widely separated.

The 6 species of *Hylobates* are difficult to distinguish from one another as they are individually variable; 4 of the 6 species have colour phases that vary with age and sex. *H. concolor*, for instance, is born fawn-coloured but becomes black after about 6 months and remains so until, on reaching maturity at about 5–7 years, the ♀ again becomes fawn, a small patch on the crown remaining black; the ♂ remains black all over, sometimes with white or fawn cheek patches. *H. hoolock*, the largest species, shows similar phases; grey at birth, both sexes gradually change to black. At puberty, the ♀ becomes brown, the ♂ remaining black with white "eyebrows" and a large preputal tuft. Apart from *H. lar pileatus* from S.E. Thailand and Cambodia (see Plate 51 for ♀ and infant: ♂ is mainly black), *H. lar* and *H. agilis* show no sexual dimorphism; ♂ and ♀ may be black or buff. In black specimens, the white hands and feet of *H. lar* contrast with its black limbs ("white-handed"); the contrast is less apparent in buff specimens. These can be confused with buff specimens of *H. agilis* in which the extremities

† See Taxonomic Notes, Part III, p. 374.

are always the same colour as the coat; dark specimens of *H. agilis* are thus "dark-handed". Both species have a pale brow-band which often extends round the face to form a complete ring of white hairs.

*H. concolor*¹⁰ is distinguishable by having a crest of erect hairs on the crown (elongated at the middle of the crown in ♂, at the sides of the crown in ♀) and no pale brow-band. In the other 5 species, the crown hairs are directed smoothly backwards. Small throat-sac present in ♂ *H. concolor*.¹⁰

H. moloch shows extreme variability in colour from black to silvery grey¹¹ but is generally grey-brown with pale brow-band and darker shading on crown and chest. Neither *H. moloch* nor *H. klossii* show colour phases; the latter is entirely black and the coat much less dense than that of the other species. In this character *H. klossii* resembles *Symphalangus*.¹⁹

Weights and Dimensions^{8, 12, 13, 14, 15, 16}

Body weight range (g)	4300–7928 (41 ♂)	4110–6800 (30 ♀)
Head and body length range (mm)	403–635 (62 ♂)	408–622 (38 ♀)

Schultz (1956) gives 93.5% (♀ weight in % of ♂ weight) on 94 specimens.

Internal Characters

For fuller account of anatomy see Bischoff (1870); Kohlbrügge (1890); Keith (1891, 1896); Sonntag (1924); Schultz (1930, 1933b, 1944); and, for anatomy of hand see Jouffroy and Lessertisseur (1960). SKULL: Ovoid neurocranium, moderately large nuchal area and moderate to slight prognathism. Sagittal crests usually lacking but occasionally seen in both sexes of *H. lar*,²⁰ associated with below average cranial capacity and high palatal index. Cranial capacity ranges between 82–125 cc (*H. lar*),²⁰ being lowest in *H. klossii*.¹⁹ Bony palate long (50–54% skull length).¹⁹ Orbits very large,⁴⁷ frontally directed, having a prominent, well-buttressed, lateral margin; buttressing of superior border produces strong brow ridges (relatively reduced in *H. concolor*) which are *not* continuous across midline. Mastoid process absent; occipital condyles lie well behind external auditory meatus in adult. VERTEBRAL COLUMN: Intermediate between Old World monkeys and Pongidae in thoraco-lumbo-sacral vertebra number.¹⁸ UPPER LIMB: Bones of upper limb extremely long and slender (see LIMB PROPORTIONS, Part III, p. 394); hand is long and narrow with deep cleft between index and thumb. An os centrale is usually present as separate element in carpus; trapezio-metacarpal joint surface is of unique shape among catarrhine primates, the saddle articulation being absent.²¹ The thenar muscles are aberrant, deep head of F.P.B. is absent as is oblique head of A.P.²² For the many muscular specializations of upper limb, see Straus (1949).²³ LOWER LIMB: Webbing between 2nd, 3rd and 4th toes frequently present in *H. klossii* and occasionally present in other species (cf. *Symphalangus*).¹⁹ GENITALIA: Sexual skin absent. Penis short and inconspicuous; scrotum absent except in *H. concolor*;¹⁰ long, grooved clitoris in *H. concolor* and *H. booblock*.^{24, 51} DENTITION: D.F. $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} = 32$. INCISORS: small and slightly procumbent. CANINES: long and sabre-like, there being slight dimorphism in size between the sexes;^{20, 25} diastema in upper jaw for lower canine. PREMOLARS: upper and lower—bicuspid. 1st lower premolar—sectorial. MOLARS: Upper—quadricuspid showing typical hominoid pattern. Lower—quincuspid. M_3^2 show a marked tendency to reduction;¹⁹ see also Eckardt (1930).



Genetic Biology

CHROMOSOMES:²⁷ $2n=44$. (*H. lar*, *H. booleck* and *H. agilis*). Karyotypes of *H. lar* and *H. booleck* are identical: 38 metacentrics; 6 subterminals; 0 acrocentrics. X sex-chromosome is a metacentric; Y sex-chromosome is a minute indeterminate structure (*H. lar*).²⁸ P.T.C. TASTING:³⁰ 46% tasters (26 specimens—*H. lar*). HAEMOGLOBINS:³¹ Hb pattern appears to be slightly different from human A. Haemoglobin polymorphism noted. IMMUNOCHEMISTRY: See Goodman (1962, 1963). BLOOD GROUPS: A, B and AB groups identified. Sex-linked Xg^a antigen as in man.²⁹

BEHAVIOUR

Locomotor Behaviour⁹

AUTHORS' CLASSIFICATION: Brachiation. Arm swinging (in *H. lar*) constitutes major (90%), but not sole, means of arboreal locomotion; other patterns include climbing, bipedal walking on branches with or without support by arms. During brachiation, legs are flexed under the body and the arms move alternately; leaps in a downward direction up to 15 m. (Fractured limbs are commonly found in wild-shot specimens.) Bipedal walking on the ground and very occasional quadrupedalism. See also Straus (1941), Avis (1962), Napier (1963). Unable to swim.⁹ LIMB PROPORTIONS: See Part III, p. 394, for Indices.

Hand Function

Hand—prehensile. Thumb—opposable. During brachiating locomotion, thumb is not used but is employed during climbing trunks of trees and thick branches; also used for manipulation of food and grooming. HAND PROPORTIONS: For Indices, see Part III, p. 401.

Resting Posture⁹

Hylobates sleep with the knees bent up to the chin, the hands folded on the knees and the face buried between the knees and chest. The thick fur is impenetrable by rain and the hunched position retains body heat. They sometimes lie supine on a broad branch.

Social Behaviour

Observations are largely those of Carpenter on *H. lar* (1940). GROUP SIZE:⁹ from 2 to 6 individuals, consisting of an adult ♂ and ♀ and up to 4 young. Occasionally an old senile ♂ may be retained within the group. Solitary animals can be old isolates or young adult animals splitting away from the parent group, exploring for a suitable mate. RANGE AND TERRITORIALITY:⁹ *Hylobates* occupy and defend sections of the forest which must be considered three-dimensionally: the acreage required by a group depends on the height of the forest as well as on the number in the group; Ellefson (in press) estimates this to be about 250–300 acres per group. *Hylobates* range freely within their territory, often encroaching on to common land between two territories, but migration is restricted. VOCALIZATION: (*H. lar*): A hooting call of rising inflection, rising pitch and increasing tempo is heard most often in the early morning and again less frequently in the afternoon. Other calls include a loud discrete, high-pitched note which operates as an alarm call; a number of intra-group calls have been recognized associated with greeting behaviour, play and group movement. There is very considerable variation in calls between species. FACIAL EXPRESSION: In friendly



greeting, the corners of the mouth are drawn back, revealing the teeth, and the tongue is sometimes protruded. In anger, the mouth is opened and closed repeatedly, smacking the lips and snapping the teeth together. Snarling, which is also exhibited, is interpreted as an intention movement of biting.³⁷ INTER-GROUP BEHAVIOUR: Policing of territorial boundaries and the common land between territories leads to almost daily conflicts in which vocalization, confrontation and chasing by the adult males are the main components. Actual fighting has only rarely been observed.^{9, 25, 48} INTRA-GROUP BEHAVIOUR: Male dominance does not exist within the group; ♀ is equally dominant in vocalization and intra-group control, also in sexual behaviour (correlated with lack of sexual dimorphism). Strong antagonism exists between two adults of the same sex. GROOMING: Mutual grooming is important as a social activity and as a hygienic function, keeping the fur clean and free from ecto-parasites. The "service" of grooming is frequently alternated between two animals. Hands and feet may be used to part the dense woolly hair and the teeth are sometimes used to remove particles from the skin. SEXUAL BEHAVIOUR: Copulation of *H. lar* in the wild has been described by Carpenter. Observations on captive pairs include *H. concolor*³⁸ and *H. moloch*;³⁹ in the latter, copulation was observed throughout the menstrual cycle and even during pregnancy.

REPRODUCTION AND DEVELOPMENT

REPRODUCTIVE CYCLE:^{40, 41}

Species	Duration of cycle in days		Duration of bleeding		No. of cycles observed
	Extremes	Mean	Extremes	Mean	
<i>H. lar</i>	21-43	29.76 ± 4.12	2-5	2.38 ± 0.54	17
<i>H. hooleck</i>	20-33	27.83 ± 4.07	2-4	2.6	6

There are no sexual skin changes, but there are some changes in the colour, degree of eversion and turgidity of the labia. GESTATION PERIOD: circa 210 days.¹⁷ There is no discrete birth season. *Hylobates* give birth to one young, usually at two-yearly intervals. The eyes are open at birth and the body and limbs are bare. The infant is therefore very dependent on the mother for warmth and she holds it between her flexed thighs and abdomen, forming a furry nest.⁹ From the first day, it can cling to her unaided.⁴² DURATION OF LACTATION is not precisely known; infant is dependent on the mother for about 2 years.⁴³ First deciduous teeth are cut at about 5 weeks; last permanent teeth at 8½ years.¹⁷ Sexual maturity is reached between 5-7 years (*H. concolor*);^{5, 44} between 8-10 years (*H. lar*);⁹ *H. hooleck*—about 7 years.⁴¹ The growth and development of an infant ♀ hybrid gibbon (*H. lar* × *H. moloch*) has been described by Rumbaugh (1965a).

CAPTIVITY

The lifespan is thought to be about 33 years.⁴⁵ LONGEVITY RECORD:⁴⁶ 31 years 6 months,

H. lar, Philadelphia Zoological Garden. BIRTHS IN CAPTIVITY: 66 births were recorded in World Zoos between 1959-63.⁵⁰ Although, when young, *Hylobates* can make gentle affectionate pets, they develop strong antagonisms on reaching maturity—also long canine teeth—which make them in adult life extremely dangerous.

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MACACA† Lacépède, 1799

Macaques

12 species: 46 subspecies^{1, 2, 3, 4}

<i>M. sylvana</i> (Type species)	Barbary ape	0 subsp.
<i>M. sinica</i>	Toque monkey	3 subsp.
<i>M. radiata</i>	Bonnet monkey	2 subsp.
<i>M. silenus</i>	Lion-tailed macaque	0 subsp.
<i>M. nemestrina</i>	Pig-tailed macaque	4 subsp.
<i>M. fascicularis</i> [= <i>M. irus</i>]†	Crab-eating monkey	21 subsp.
<i>M. mulatta</i>	Rhesus monkey	4 subsp.
<i>M. assamensis</i>	Assamese macaque	2 subsp.
<i>M. cyclopis</i>	Formosan rock macaque	0 subsp.
<i>M. speciosa</i> †	Stump-tailed macaque	4 subsp.
<i>M. fuscata</i>	Japanese macaque	2 subsp.
<i>M. maurus</i>	Celebes or Moor macaque	4 subsp.

GEOGRAPHICAL RANGE

North Africa; Gibraltar (introduced); Asia from E. Afghanistan and Tibet to China, Japan and Formosa, south to India and Ceylon; throughout S.E. Asia including Sumatra, Java, Borneo, Philippines and Celebes, and many offshore islands. Limits of genus: 41° 20' N.–11° S.: 10° W.–128° E. From sea-level to 13,000 ft (4000 m).⁵ *M. fascicularis* has been introduced into Mauritius,⁶ and *M. mulatta* into Cayo Santiago, West Indies.⁷ See p. 403 for range of species.

ECOLOGY

HABITAT: From tropical rain forest, monsoon forest and mangrove swamps to montane forest of the Himalayas and temperate forests of China and Japan; also grassland and dry areas of scrub and cactus in India and Ceylon. *Macaca* are partly arboreal and partly terrestrial, usually sleeping in trees to avoid predators, but also frequenting cliffs and rocky places. *M. cyclopis* prefers cliffs and rocks by the seashore to the forest.⁸ *M. fascicularis* typically lives near the coast in tidal creeks and mangrove swamps. In India, *M. mulatta* traditionally inhabits temples and villages.⁹ In common with most species, *M. mulatta* raids plantations and cultivated fields for food; *M. silenus* is relatively shy, inhabiting secluded parts of monsoon forest of the Western Ghats.¹⁰ **ACTIVITY RHYTHM:** Diurnal. **DIET:** Fruit, roots and young leaves; insects, grubs; crops such as rice, maize, potatoes and sugar-cane; molluscs and crustaceans (*M. fascicularis*, *M. cyclopis*).

MORPHOLOGY

External Characters

Medium to large, heavily-built, monkeys with robust limbs of almost equal length. Coat is of various shades of brown, or black. Low brow ridges are continuous over nose in ♂♂. Muzzle moderately prognathous and rounded. Nose does not extend beyond upper lip; nostrils, separated by a narrow septum, are directed obliquely outwards and downwards. Ears typically

† See Taxonomic Notes, Part III, p. 375.





bare; upper posterior margin of pinna is angled. Ischial callosities conspicuous and not fused across midline except in *M. maurus* ♂ where they are almost confluent. Considerable sexual dimorphism in body size. In colder climates, the fur grows very long and thick. Cheek pouches are visible when full of food (see Plate 69, Adult ♀).

Colour and texture of coat, colour of face, characters of tail and external genitalia show considerable variability within the genus; for full details of inter-specific variation in external characters see Part III, Data on Macaques, p. 405.

Weights and Dimensions

Body weight range ^{6, 10-22} (g)	3500-18,000 (82 ♂♂)	2500-16,300 (63 ♀♀)
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According to available records, *M. fascicularis* is the lightest species and *M. fuscata* the heaviest. Body weight of ♀ in % body weight of ♂: *M. fascicularis* 63.9%; *M. mulatta* 69%.²³ See Part III, p. 406 for detailed weights and dimensions of all species.

Internal Characters

For details of the anatomy of *Macaca*, reference should be made to works of Pocock (particularly 1925a) and to Hartman and Straus (1933). Only characters of special interest are noted here. **SKULL:** Facial and jaw regions are relatively heavy compared with calvarium but prognathism is only moderate. Orbits are frontally facing and in ♂ surmounted by a low supra-orbital torus. Lacrimal bone extends slightly on to face as in *Papio*. Paranasal depressions are lacking (cf. *Cercocebus*, *Papio*). External auditory meatus long as in all Old World monkeys. **VERTEBRAL COLUMN:** C.7/T.12/L.7/S.3. Manubrium and sternum, rodlike; five sternbrae united by cartilage. **FORELIMB:** Os centrale present; paired sesamoids opposite each metacarpo-phalangeal joint. Thenar muscles well developed including a deep head of flexor pollicis brevis; flexor pollicis longus not discrete from deep flexor group. D.F.: 3.4.2.5.1. **HINDLIMB:** Pelvis long and narrow with broad flat ischial tuberosities, widely splayed in the ♀. Femur bears a long, prominent greater trochanter; third trochanter absent and linea aspera poorly defined. Foot has digital formula 3.4.2.5.1., the hallux is abducted and of medium length as in all Old World monkeys (but particularly large in *M. nemestrina*).²⁴ **DIGESTIVE SYSTEM:** Cheek pouches well developed as in all Cercopithecinae; they form discrete muscular mucous-lined pockets extending under mandibular rami; pouch musculature contracts to propel food back into mouth; over-distension of pouches leads to ineffectiveness of voluntary musculature and pouches must be emptied manually by external pressure.²⁶ Stomach is a simple sac (cf. Colobinae); caecum is conical in form and lacks appendix; colon is long, mobile, tortuous, sacculated and has a mesentery throughout its length. **GENITALIA:** Pendulous scrotum and penis situated anteriorly over symphysis pubis;²⁷ typically glans penis is short and rounded with a short thick baculum. Glans is longest in *M. mulatta* and shortest in *M. fascicularis*. In *M. radiata* and *M. sinica*, penis is large and has specializations of the glans; in *M. speciosa*, the glans is particularly long and tapering, supported throughout its length by a long thin baculum.^{24, 28} **NERVOUS SYSTEM:** Brain is large and shows similar fissural pattern to certain New World monkeys, e.g. *Cebus*. Cerebellum is large with expanded lateral lobes, floccular lobes are distinct and occupy a pit in petrous temporal bone, the subarcuate fossa. **DENTITION:**²⁹ D.F.: $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} = 32$. **INCISORS:** Upper central incisors broader than laterals. **CANINES** show sexual dimorphism being strongly developed in ♂ and barely projecting in ♀. **PREMOLARS:** Bicuspid with relatively large buccal cusp; PM.₁ is adapted for shearing against upper canine ("sectorial"). **MOLARS:** All molars are



quadricuspid except $M_{\frac{3}{3}}$ which bears an extra cusp on talonid; anterior and posterior cusps united by transverse crests ("bilophodonty"). DECIDUOUS DENTITION: D.F.: $\frac{2}{2} \frac{1}{1} \frac{2}{2} = 20$. Central incisors appear at 2-3 weeks, canines and 1st milk molars at 12-14 weeks; 2nd milk molars at 23-25 weeks.¹²

Genetic Biology

CHROMOSOMES:^{30, 88} $2n=42$. KARYOTYPE of *M. mulatta*: 0 acrocentrics, 18 metacentrics, 22 subterminals, $X=M$, $Y=M$ or A . Chiarelli (1962b) has analysed the chromosomes of all species of *Macaca* (except *M. cyclopis*) and compares the karyotypes with those of *Cynopithecus*, *Papio*, *Theropithecus* and *Cercocebus*, all of which have a diploid number of 42. In *Macaca* the X chromosome shows a great deal of variation; the Y is always very small and the centromere cannot be distinguished. BLOOD GROUPS: For MN and Rh factors, see Franks (1963), and for recent investigations on A-B-H and Lewis substances, see Wiener, Moor-Jankowski and Gordon (1966); also Owen and Anderson (1962). HAEMOGLOBINS: *M. mulatta* show transferrin type B.B. and Haptoglobin type 1-1.³⁵ Mobility on starch gel electrophoresis of *M. mulatta* and *M. nemestrina* is similar to that of man.³⁶ *M. fascicularis*: 13% have fast component P^{mi} ; 24% showed occurrence of another variant Q^{mi} .⁸⁶ SERUM PROTEINS: Marked similarity in reactions between genera of Cercopithecinae (particularly *Macaca* and *Cercopithecus*) on basis of immuno-precipitin data.³⁷ P.T.C. TASTING:³⁸ Tasters : non-tasters—80 : 11.

BEHAVIOUR

Locomotor Behaviour

AUTHORS' CLASSIFICATION: Quadrupedalism. Macaques move freely on the ground as well as in the trees. Proportionate time spent in trees and on ground varies intra- as well as interspecifically. The most arboreal species include *silenus* and *nemestrina*; the most terrestrial are *sylvana*, *cyclopis* and *mulatta*. During branch-walking the hand is plantigrade but when on the ground, it is usually digitigrade.³⁹ Bipedalism is common when hands are carrying food objects (Hewes, 1961). LIMB PROPORTIONS: For Indices, see Part III, p. 394.

Hand Function

Hand prehensile, thumb fully opposable. Precision grip between thumb and index finger well-developed. Hand used in feeding and grooming. HAND PROPORTIONS: For Indices, see Part III, p. 402.

Social Behaviour

A considerable amount of work has been done on the behaviour of the macaque both in the laboratory and in the field. For principal references to behaviour studies, see the following:

	Laboratory	Field	Captivity
<i>M. mulatta</i>	40-48	7, 9, 19, 57-60	51-53, 55, 56
<i>M. fuscata</i>	—	61-69	—
<i>M. nemestrina</i>	49	—	50
<i>M. radiata</i>	—	70, 71	—
General	—	72	54

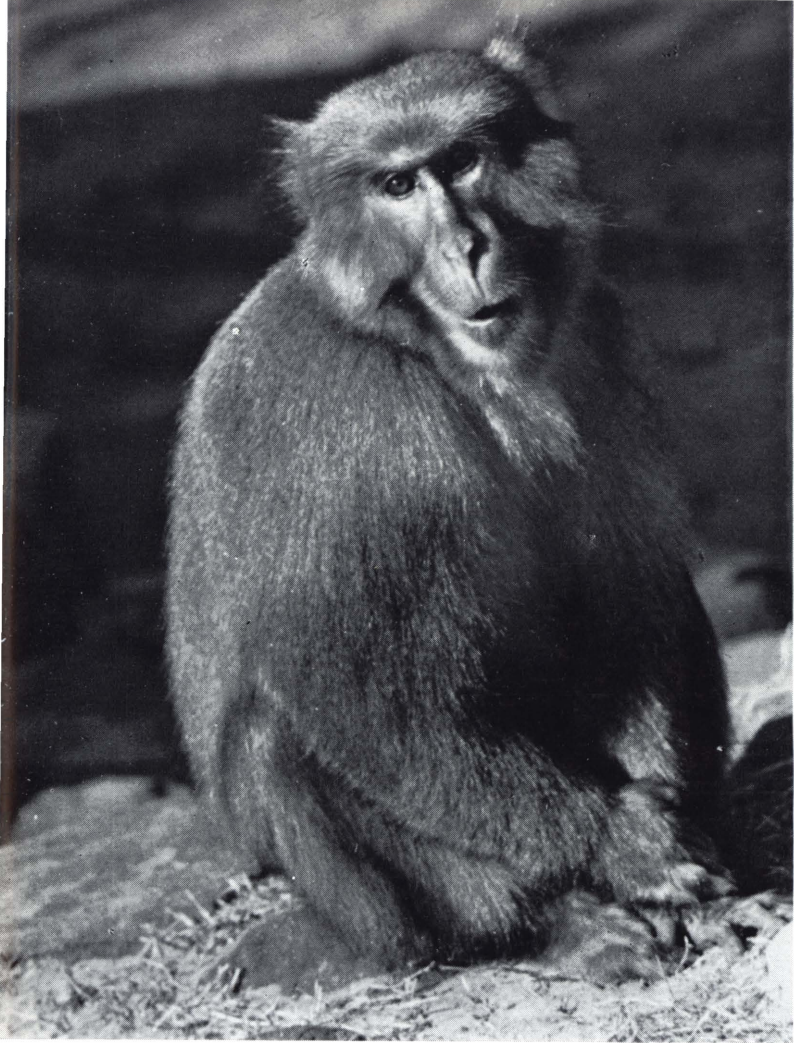


PLATE 67. Above: *Macaca fuscata*, adult ♂ (by courtesy
of Masao Kawai); Below: *Macaca sylvana*

The following is an abstract of some of the above-mentioned field studies. Social behaviour in macaques is subject to many interspecific variations; intraspecific differences are generally associated with differences in habitat. *Macaca* live in large groups in which there is usually more than one adult ♂.

AVERAGE GROUP SIZE:

<i>M. mulatta</i>	N = 17.6	(399 groups). Temple and forest-dwelling macaques have on the average larger groups (41.9, 49.8) than railside, roadside and village dwellers (11.4, 15.1, 17.4). ⁶⁰
<i>M. radiata</i>	N = 34.5	Range: 6-58 (4 groups). ⁷¹
<i>M. fuscata</i>	N = 194	Range: 26-570 (10 observations). Since the provisioning of <i>M. fuscata</i> , begun in 1952, group size has tended to increase. ⁶⁷
<i>M. assamensis</i>	N = 12, 26	(2 observations). ⁷³
<i>M. fascicularis</i>	N = 6-10	in tropical rain forest: 30 in nipa-mangrove swamp. ^{74, 75}

COMPOSITION OF GROUPS:

	Adult ♂	Adult ♀	Juvenile	Infant	Total	Adult sex ratio	N
<i>M. mulatta</i>	3.7	7.7	1.5	4.5	17.6	1♂ : 2.1♀	399 groups ⁶⁰
<i>M. radiata</i>	12	10.25	5.75	6.5	34.5	1♂ : 0.85♀	4 groups ⁷¹
<i>M. assamensis</i>	2 4	6 10	2 8	2 4	12 26	1♂ : 2.7♀	2 groups ⁷³
<i>M. fuscata</i>						1♂ : 1.4♀	10 observ. ⁶⁷

DOMINANCE: Clearcut dominance hierarchies are formed among ♂♂, and more obscurely among ♀♀. Relationships may be friendly or antagonistic according to individual personality and/or kinship.^{65, 68} Subgroups are formed within the group; central area is occupied by dominant ♂♂, plus ♀♀ and infants; in *M. mulatta*⁵⁸ and *M. fuscata*,⁶¹ subordinate ♂♂ live in a peripheral area, or outside the group as solitary ♂♂. In *M. radiata* no ♂♂ were excluded from the central area, neither were solitary ♂♂ nor subgroups observed.⁷¹ **HOME RANGE AND TERRITORIALITY:** Home ranges of up to about 3 sq miles (8 sq km) may overlap those of other groups (*M. fuscata*, *M. mulatta*). Inter-group behaviour is antagonistic but subordinate groups tend to avoid dominant groups so inter-group fighting is relatively rare. In an urban area however 24 severe fights were seen in 85 days observation (*M. mulatta*: 4 groups).⁶⁰ *Macaca* do not defend precise territories; sleeping trees and sites may be within the range of other groups (*M. mulatta*).



PLATE 68. *Macaca radiata*, adult ♂ and adult ♀ with twins (by courtesy of Phyllis Jay)

Macaca live in the same habitat as *Presbytis* and, in interactions, *Macaca* are dominant, usually without conflict.^{71, 75} COMMUNICATION: Consistent with their complex social life, *Macaca* are capable of communicating a wide range of emotions; over 30 vocal sounds have been described by Itani (1963) for *M. fuscata*. Facial expressions have been described by van Hooff (1962) among them eyebrow-raising associated with retraction of the scalp, lip-smacking, and the “flehmen” face. Subordination in *Macaca* is indicated by directing the hindquarters towards a dominant animal (“presenting”); mounting the hindquarters so presented and carrying the tail erect are dominance gestures. Branch- or tree-shaking is an aggressive gesture seen in *M. fuscata*⁶⁶, *M. mulatta*¹⁹ and *M. radiata*.⁷⁰ SOCIAL GROOMING: Incidence varies seasonally. Most common patterns are ♂-♀ grooming during consort relationships, and mother-young grooming (*M. fuscata*,⁶⁵ *M. mulatta*).⁶⁰ In *M. radiata*⁷¹ (and in *M. fuscata*⁶⁵ during the non-breeding season) ♂-♂ and ♀-♀ grooming are more common than heterosexual grooming.



PLATE 69. *Macaca sinica*, L. to R. Adult ♀ with infant, young ♂, adult dominant ♂ (by courtesy of Phyllis Jay)

PLAY: *M. mulatta*: infants and juveniles play in their respective age groups.⁶⁰ *M. fuscata*: from 8 months, infants and juveniles play with others of the same sex.⁶¹ *M. radiata*: play continues into adult life in ♂♂ only.⁷¹ Play is usually preadaptive and consists of mounting, wrestling, biting and chasing, but *M. mulatta* invent apparently non-functional games, i.e. 20–30 ft jumps from trees into pools of water.⁵⁸ SEXUAL BEHAVIOUR of *M. mulatta* has been described by Carpenter (1942); that of *M. fuscata* by Tokuda (1961–62); and that of *M. radiata* by Simonds (1965). In *M. mulatta* and *M. fuscata*, consort relationships are formed; copulation consists of several mountings before ejaculation. (For comparative behaviour, see Tokuda, 1961–62). In *M. radiata*, however, consort relationships are not formed and copulation consists of only one mounting;⁷¹ similar copulatory behaviour has been observed in *M. fascicularis*.⁷⁶ Incidence of copulation varies seasonally;⁷⁷ in *M. fuscata* it is restricted to October–April, with peak

PLATE 70. *Macaca fuscata*; above: 8-year old ♀ running bipedally; below: erect posture and bipedal walking in the sea (by courtesy of Masao Kawai)



frequency January and February; in *M. radiata*, copulation was observed throughout the year, with peak frequency October and November. Copulation between mother and son has never been observed in *M. fuscata*.⁷⁸

Macaca are highly social animals. Male role is to lead, organize progression, settle quarrels—in fact to impose discipline on the group. Female role is to produce and rear young—usually once a year—and to continue a relationship with them after weaning, thus providing continuity and bonds of kinship within the group (cf. *Presbytis*). Paternity is not recognized in macaque society, but ♂♂ occasionally show “paternal” care towards infants (*M. fuscata*,⁶³ *M. sylvana*⁷⁹ and, in the laboratory, *M. radiata*).⁴²

REPRODUCTION AND DEVELOPMENT

For comparative data on reproduction in Macaque species, see Table 4, p. 406, Part III. Menstrual cycles occur throughout the year; where data are available, oestrus appears to be seasonal. Typical manifestations of oestrus have been described in Table 2, showing specific variation of adult macaques (see Part III, p. 405); there is great variability between individuals but sexual skin changes are usually more pronounced in adolescent than in older ♀♀. Sexual skin of *M. sinica* and *M. radiata* shows no change during oestrus; a copious discharge of clear strong-smelling mucus from the vagina occurs not only during periods of sexual receptivity but also frequently throughout the cycle.^{80, 82}

Seasonal enlargement of the testes of *M. mulatta*, accompanied by increased reddening of the sexual skin of the ♂, has been observed to correspond with peak frequency of copulation.⁸³

Spiegel (1954) has described the birth of *M. fascicularis*. Hartman (1928) reported the birth of *M. mulatta*; at birth, eyes closed, but open within 2 hours; no teeth visible.⁸⁴ For age estimation from dentition (*M. mulatta*), see Schultz (1933a). *Complete deciduous dentition* at 6 months; *1st permanent molars* erupt at 1 year 8–9 months; *complete permanent dentition*: 7–8 years or later. Although sexual maturity is reached at about 4 years, full growth is not complete until 10th year in ♂♂, 6th year in ♀♀ (*M. fascicularis*).²¹

CAPTIVITY

Macaca are very adaptable and have proved relatively easy to keep and breed in captivity. All 12 species have been kept successfully in Zoos. **LONGEVITY RECORD:**⁸⁵ Longevity for the genus: *M. sinica*, 29 years 4 months, Colombo Zoo. For longevity records of species, see Macaque section, Part III, p. 407.

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MANDRILLUS† Ritgen, 1824 Drills and Mandrills

2 species: 2 subspecies

M. sphinx (Type species)
M. leucophaeus

Mandrill
Drill

0 subsp.
2 subsp.

GEOGRAPHICAL RANGE¹

Africa. Range of both species is relatively limited and is confined to high forest regions between the Cross R. in S.E. Nigeria and the R. Congo. Both species are found in Cameroun, S. of Sanaga R., Gabon, Congo (Brazza) and Spanish Guinea. Drills, alone, extend westward to the Cross R.; also Fernando Póo.²³

ECOLOGY

HABITAT:² Inhabitants of rain forest but also of mountainous regions of Cameroun. Usually seen in rocky clearings of forest floor. Principally ground-living but feed and sleep in trees. ACTIVITY RHYTHM: Diurnal. DIET:* Omnivorous.

MORPHOLOGY

External Characters^{3, 4}

Large animals showing well-marked sexual dimorphism. Both sexes of both species have massive muzzles with prominent, longitudinal, fusiform, rugose swellings on either side of nose; these swellings are smaller in drills than in mandrills. Eyes are deepset, ears flesh-coloured in *M. sphinx*, black in *M. leucophaeus*. The coat of ♂ mandrill is long and thick, dark brown to charcoal grey in colour, with fringes of yellow and orange. The nose and nostrils of the ♂ are lacquer-red and the longitudinal paranasal swellings are a brilliant electric blue. Cheek tufts are white and the beard yellow to orange; hair rises from ridge on brow to crest on top of head; the ♀ mandrill lacks bicoloured mask of the ♂. The genitalia of the ♂ mandrill correspond, broadly speaking, to the colour combination of the face.⁵ The circumanal region is red; lateral to the callosities there is a blue patch fading peripherally to lilac; posterior scrotum lilac, anterior pink; pubic region scarlet and glans penis pink. Perineal colouration is not developed in ♀.⁶

The coat of the drill is olivegreen and the mask is jet black. Beard and cheek tufts white. The perineal area of the ♂ drill shows even more vivid colouration than that of the mandrill, and of a somewhat metallic nature. Sexual swelling of the ♀ drill resembles that of *Cercocebus* and is relatively unpigmented.⁶ Both species have moderate ischial callosities, pink in colour, which, in ♂♂, are fused across the midline as in *Papio*. The tail in both species is stumpy and the forelimbs appear longer and stronger than the hindlimbs giving the trunk a backward-sloping inclination.

Weights and Dimensions

Body weight (g)	<i>M. sphinx</i>	19,522 (♂)		
Head and body length (mm)	<i>M. sphinx</i>	810 (♂)	<i>M. leucophaeus</i>	700 (♂)
Tail length (mm)	<i>M. sphinx</i>	70 (♂)	<i>M. leucophaeus</i>	120 (♂)

† See Taxonomic Notes, p. 375.

Internal Characters

For principal anatomical characters, see *Papio*. Distinguishing features are noted here. **SKULL:** Massively constructed, markedly prognathic, heavy bony swellings on maxilla. In the ♂ a supra-orbital torus and a sagittal crest are present. Mandible is long, stout and curved along its lower border and almost wholly lacking an angle. Palate is wide in front and narrow at the back, thus the premolar tooth series converge posteriorly; this pattern is quite unlike the parallel tooth-rows of *Papio*. **HANDS:** Unlike those of *Papio*; the length of the hand relative to the length of the arm is greater, the palm is broader and the fingers and thumb are longer (see Hand Proportions, Part III, p. 402). **FEET:**⁷ Differ from those of *Papio* in the relatively greater length of the digits especially the big toe which is strikingly enlarged. Clearly the characters of the hand and foot are adaptations to bring about a greater span in the extremities in relation to branch-walking habits.¹¹ **DENTITION:** D.F.: $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} = 32$. Incisors are rather small in both upper and lower jaws. Wide diastema between upper incisors and canine. Molars are similar in form to those of *Papio* but differ in the curvature of the tooth-rows. Size increases from M.1-3 in both jaws.

Genetic Biology

CHROMOSOMES:^{9, 22} $2n = 42$ (♂ + ♀ *M. sphinx*, ♂ + ♀ *M. leucophaeus*). **P.T.C. TASTING:**¹⁰ Tasters: non-tasters = 48: 8 (86%). **BLOOD GROUPS:**²⁵ Drill shows human A. Lewis substance absent in saliva.

BEHAVIOUR

Locomotor Behaviour

AUTHORS' CLASSIFICATION: Quadrupedalism. Mandrills show a digitigrade gait of forelimbs both on the ground and in trees when branch-walking.¹¹ **LIMB PROPORTIONS:** For Indices, see Part III, p. 394.

Hand Function

Hand prehensile, thumb opposable. High "opposability" index (see Hand Proportions in Part III) indicating well-developed index-finger to thumb precision grip as in *Papio*. Precision and power grip well differentiated.

Social Behaviour

At present no field studies are available and information on drills and mandrills in the wild is wholly anecdotal.^{12, 13, 14}

Psychobiology

Darwin (1872) and Elliot (1913) state that colour of facial and perineal skin of mandrill is intensified when animal becomes excited. These observations have not been confirmed by Hill (1955).

REPRODUCTION AND DEVELOPMENT

Little is known of the reproductive cycle; mean menstrual cycle length: 32.6 days \pm 0.9 days (*M. leucophaeus*).²⁴ Swelling of the sexual skin observed in both species.²⁴ **GESTATION PERIOD:** 245 days.¹⁷ **HYBRIDS:**^{18, 19} A number of ♀ *Mandrillus* crosses with *Cercocebus*, *Macaca* and *Papio* reported in captivity; fewer ♂ *Mandrillus* crosses recorded.



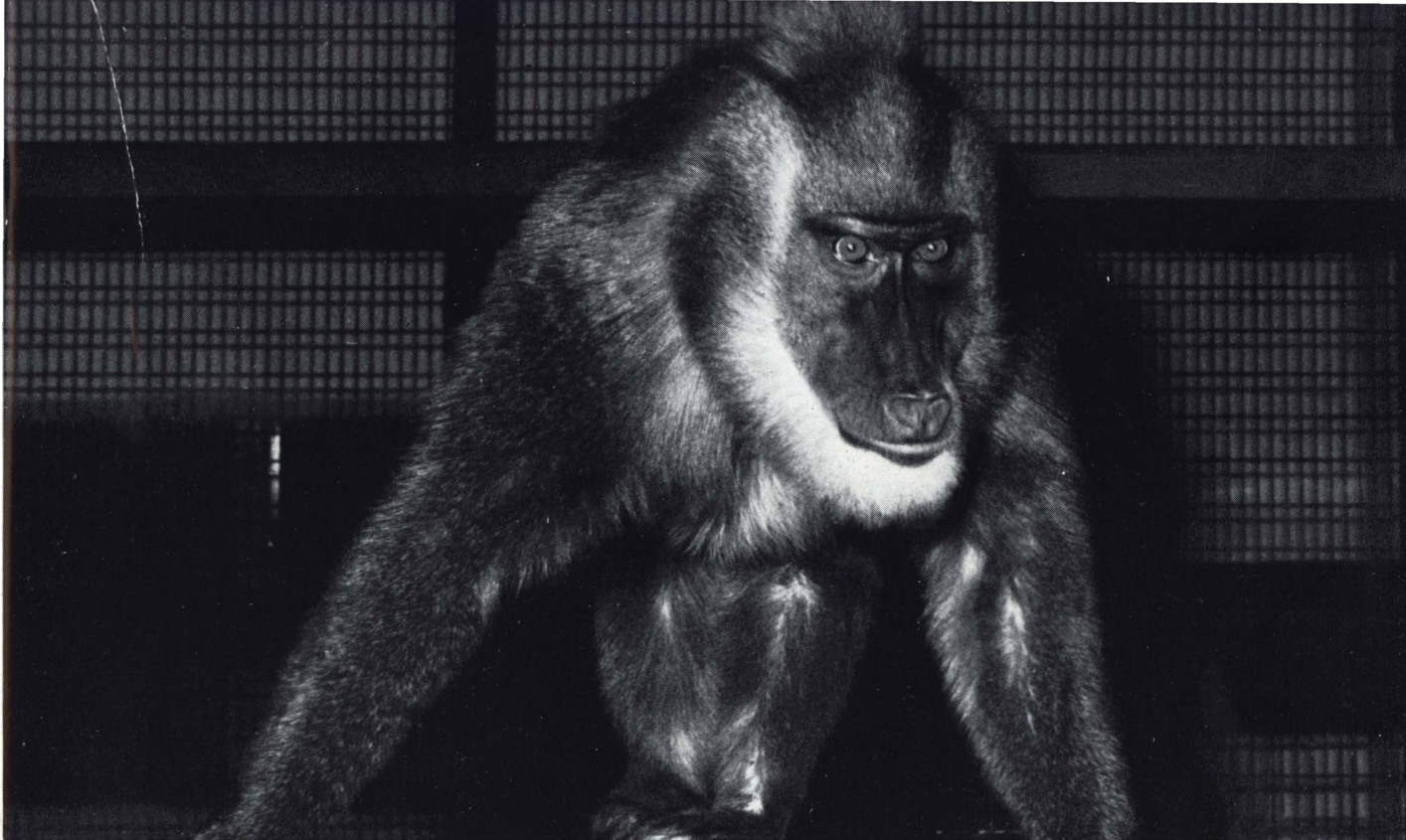


PLATE 72. Drill, *Mandrillus leucophaeus*, ♂ aged 7 years (by courtesy of Doris M. Sorby)

CAPTIVITY

Births in captivity are now very common.²⁰ LONGEVITY RECORD (up to 1962):²¹ *M. leucophaeus*, 28 years 6 months, Milwaukee Zoo, U.S.A.; *M. sphinx*, 27 years 3 months, National Zoological Park, Washington.

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PLATE 71. Mandrill, *Mandrillus sphinx*, young ♂ aged 3 years (by courtesy of Doris M. Sorby)

2 species: 3 subspecies^{1, 2, 3}

<i>P. troglodytes troglodytes</i>	Tschego
<i>P. troglodytes verus</i>	Common or masked chimpanzee
<i>P. troglodytes schweinfurthii</i>	Eastern or long-haired chimpanzee
<i>P. paniscus</i>	Pygmy chimpanzee

N.B. The "common chimpanzee" in Great Britain is the familiar name for *P.t. verus*; in Europe, *P.t. troglodytes* is regarded as the "common chimpanzee".

GEOGRAPHICAL RANGE^{1, 3, 4, 5, 6, 7}

P.t. verus: W. Africa. Forest regions from Sierra Leone and French Guinea eastward to R. Niger. Latitudinal limit: 10° N. *P.t. troglodytes*: Central Africa. E. of R. Niger to R. Congo where it is limited to the W. bank. *P.t. schweinfurthii*: Central and E. Africa. Extends from the E. bank of the R. Lualaba and S. of R. Ubangi, as far E. as Lake Victoria in northern part of range and Lake Tanganyika in southern part. *P. paniscus*: Limited to enclave formed by Congo and Lualaba Rivers. TYPE LOCALITY: Befalé, S. of Maringa River.

ECOLOGY

HABITAT:^{7, 8, 9} Tropical rain forest, forest savannah mosaic and deciduous woodland in hilly country; also found in montane forest up to 10,000 ft (3048 m). Secondary forest in Sierra Leone. Habitat is arboreal for approximately 50–75% daylight hours; sleeping hours are spent in tree-nests, newly built every night and seldom less than 15 ft from the ground. DIET: Primarily vegetarian, consisting of fruits, leaves, palm-nuts, bark, seeds and stems.^{8, 9, 10} Less common components include galls, termites and ants,^{9, 11} native-cultivated fruits,^{12, 13} e.g. paw-paw, meat^{9–11} and fish.^{13*} ACTIVITY RHYTHM: Diurnal.

MORPHOLOGY

Weights and Dimensions

	♂	♀	♀ in % of ♂
Body weight ¹⁴ (Average)	48.9 kg (2♂)	40.6 kg (5♀)	90†
(<i>P. troglodytes</i>)			
Head and body length ¹ (mm)	770–925 (7♂)	700–850 (4)	94
(<i>P. troglodytes</i>)			

† Schultz (1956) states adult ♀ weighs 87.9% adult ♂ (28 specimens).

N.B. Information on wild-shot weights is very inadequate. One authority (L. G. Smith—private communication) estimates maximum weights of ♂ and ♀ in wild to be approximately 54.6 kg. Maximum weights recorded in Zoo animals: ♂ 90 kg, ♀ 80 kg. (♀ in % ♂ based on midpoint of ranges.)

† See Taxonomic Notes, p. 375.



PLATE 78. *Pan troglodytes schweinfurthii*, young ♀

External Characters

Except for *P. paniscus*, which is of lighter build, chimpanzees are large, robust animals with pale, mottled or darkly pigmented faces, prominent ears and protrusive lips; arms are longer than legs; hand long but thumb short. Tail-less. Coat is predominantly black in colour. Juveniles are black with white tuft of hairs in anal region; mature adults have grey hairs mingling with black on lumbar region and thighs; white hairs grow on the chin in adults of both sexes. Both sexes prone to baldness in early maturity; in the ♀ the bald patch extends back as far as the vertex, in the ♂ baldness is usually limited to triangular patch on forehead. Skin of body is white, but skin of face varies with species and race, as follows:

<i>Species</i>	<i>Skin colour of face</i>
<i>P.t. verus</i>	Black pigmentation forming butterfly-shaped mask. Whole face darkens with age.
<i>P.t. troglodytes</i>	Freckled on white but may become muddy colour with age and heavily mottled.
<i>P.t. schweinfurthii</i>	White passing into a dark muddy colour with age.
<i>P. paniscus</i>	Black.

Internal Characters

For details of anatomy see Elliot-Smith (1902), Sonntag (1924), Schultz (1930, 1940b), Clark (1959). The following characters are selected principally for their known functional importance or for their value for identification. **SKULL:** Calvarium rounded, facial skeleton moderately prognathic; orbits frontally directed and surmounted by prominent and confluent supra-orbital crests. Small sagittal crest very occasionally seen in large ♂♂ and ♀♀; nuchal crest absent. Cranial capacity¹⁴ 290–500 cc (94 adults). Foramen magnum situated well posteriorly on basis cranii. **VERTEBRAL COLUMN:**¹⁸ Thoraco-lumbar vertebrae very variable in number, commonly 17: T.13, L.4. **THORAX:** Greatest diameter is transverse; body of sternum long and slender, sternbrae frequently fused. **ARM:** Humerus longer than radius. Humeral head medially directed; trochlear and capitulum separated by a prominent keel (as in all Hominoidea). Olecranon process short, head of radius rounded and shaft well bowed. **HAND:** Os centrale usually fused to scaphoid in adults; carpal tunnel deep, metacarpals long, slender with rounded heads. Phalanges curved and ventrally grooved. Pollex short. Deep head flexor pollicis brevis absent.²¹ **LEG:** Femur robust with antero-posterior curvature; sometimes longer than humerus (cf. *Gorilla*, *Pongo*). **FOOT:**²⁰ Relatively short compared to trunk length but big toe is long and stout (as in all Hominoidea except *Pongo*). **DENTITION:** D.F.: $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} = 32$. **INCISORS:** Central upper pair broad, spatulate. **CANINES:** Long, powerful, conical teeth in ♂, somewhat shorter in ♀. Upper canine separated from lateral incisor by diastema in adults. **PRE-MOLARS:** Upper: homodont and bicuspid. Lower: heterodont; anterior p.m. is unicuspid and sectorial; posterior p.m. is bicuspid. **MOLARS:** Decrease in size 1–3 (cf. *Gorilla*, *Pongo*). Upper molars are quadricuspid; lower molars bear 5 cusps (Y or “Dryopithecus” pattern), including a hypoconulid but lacking the talonid heel of catarrhine monkeys. Cusps of molars are conical. For range of variation in chimpanzee dentition.^{22, 23} **ALIMENTARY SYSTEM:**²⁴ Stomach simple and capacious; caecum as in man, with appendix. Liver is essentially a simple bilobular structure (cf. *Gorilla*) and its peritoneal attachments to diaphragm are as in man. **VASCULAR SYSTEM:** Great vessels arise from aortic arch from 2 branches, usually R and L innominate. **RESPIRATORY SYSTEM:** Extensive laryngeal air sacs are present.



PLATE 79. Above: *Pan troglodytes troglodytes*, subadult (photo by Marcel Langer); Below: *Pan troglodytes verus* (Basle Zoo)



Genetic Biology

CHROMOSOMES: *P. troglodytes* (11♂, 9♀): $2n=48^{25, 26, 27, 28, 29}$; *P. paniscus* (1♂, 2♀): $2n=48^{25}$; IMMUNOCHEMISTRY: See the studies of Goodman (1962a, b; 1963), Williams and Wemyss (1961) and Williams (1964). Serological evidence demonstrates close phyletic affinity of *Pan*, *Gorilla* and *Homo*. HAEMOGLOBINS: Serum proteins have been studied by starch gel electrophoresis by Lange and Schmitt (1963) and Buettner-Janusch and Buettner-Janusch (1964). *Pan* has Hb pattern that closely resembles that of *Gorilla* and *Homo*. BLOOD GROUPS: Groups A and O identified.³⁷ A antigen of *Pan* is not identical with either A₁ or A₂ antigens of man.³⁸ Polymorphic for MN blood factors which have been extensively studied.^{38, 39, 40} P.T.C. TASTING:⁴¹ *P. troglodytes*: 53 tasters: 17 non-tasters; *P. paniscus*: 8 tasters: 3 non-tasters.

BEHAVIOUR

Locomotor Behaviour^{8, 9, 12}

AUTHORS' CLASSIFICATION: Modified brachiation. Brachiation is quite common for short distances but frequently the feet and hands are used with the body held in upright position. On the ground (25–30% daylight hours) chimpanzees walk quadrupedally using the backs of the middle phalanges and the flat of the feet. BIPEDALISM: Bipedal standing frequently occurs to improve visual range but bipedal walking and running is relatively rare, and appears to be used in long grass, when the hands are occupied with a load or during display activities. For bio-mechanical analysis of bipedal walking, see Preuschoft (1963) and Elftman (1964), and for characteristics of gait, see Hildebrand (1967). LIMB PROPORTIONS: For Indices, see Part III, p. 394.

Hand Function

Hand prehensile, thumb opposable. Fingers disproportionately long compared with thumb which prevents precision grip between tips of thumb and index finger.⁴⁵ Power grip specially modified to grasp slender twigs and lianas.⁴⁵ Principal grip during locomotion is "hook-grip". Manipulative activity includes self-grooming, nest-building,⁴⁶ tool-using,¹¹ and in captivity action-painting,⁴⁷ etc. For dermatoglyphics, see Cummins and Spragg (1938). HAND PROPORTIONS: For Indices, see Part III, p. 402.

Resting Posture^{9, 46}

Sleep in nests on their side with knees drawn up, sometimes on back with legs extended and occasionally on stomach. Day-nesting takes place either on ground or in trees; posture is either lying on side or sitting and sprawling in relaxed postures.

Social Behaviour

The following brief account of the social behaviour of *P. troglodytes* is an abstract of a number of field studies to which reference should be made.^{8, 9, 12, 49} Principal sources are those of Kortlandt (1962), the Reynolds (Budongo Forest) and Goodall (Gombe Stream Reserve). As in the case of baboons, evidence is accumulating that behaviour of chimpanzees is subject to considerable inter- and intraspecific variation that appears to be closely related to the nature of the habitat. The literature concerning behaviour of chimpanzees in captivity is extensive;





PLATE 81. *Pan troglodytes schweinfurthii* (by courtesy of Jane Goodall and the National Geographic Society)

reference should be made to the studies of Nissen, Kohler (1925) and Yerkes (1943, 1929); for laboratory studies and for studies in zoological gardens, see Benchley (1942), Hediger (1950, 1955), Morris (1963), and Rempe (1961) (*P. paniscus*). DENSITY OF POPULATION: Approx. 3/sq mile (Gombe Stream Reserve) and 7/sq mile (Budongo rain forest). GROUP STRUCTURE AND BEHAVIOUR: NUMBERS: No stable groups. Temporary association groups in Gombe population vary in number from 2-23; in Budongo, fruit-ripening in certain trees may lead to temporary associations of small bands to form mixed groups of maximum 46. Commonest group size in Gombe and Budongo is less than 9. Largest group seen by Kortlandt was 48. COMPOSITION: Unstable. Four group "types" are recognizable: (i) adult bands composed of both sexes. (ii) male bands. (iii) Mother bands with infants. (iv) Mixed bands. Solitary ♂♂ are seen.^{8, 9} DOMINANCE: No evidence of linear hierarchy within groups but some evidence of dominance reactions between individuals; these are

relatively rare and usually between mature ♂♂. Goodall observed marked tolerance between adult ♂♂ and younger animals. The Reynolds also note infrequency of quarrelling and aggressive displays. **SOCIAL GROOMING:**⁹ Grooming is an important activity of adults. **COMMUNICATION:** Chimpanzees express themselves by means of vocalizations, facial expression, hand gesture and body posture. Goodall describes greeting and submissive gestures in detail. Both the Reynolds and Goodall describe "drumming" on tree-trunks and buttress roots. **HOME RANGE AND TERRITORIALITY:** In hilly woodland habitat of Gombe, range is 6–20 sq miles; smaller range (approx. 10 sq miles) in Budongo forest habitat. **INTER-GROUP RELATIONS:** Notable for lack of aggressiveness; groups communicate by means of loud calls; for vocalizations of chimpanzees, *see* Goodall (1965). **PLAY:** Individual play activity becomes social play during juvenile phase (3 to 8 years) and tapers off after puberty, being "replaced" by social grooming. **SEXUAL BEHAVIOUR:**⁹ Copulation may be initiated by ♂ or ♀; it usually takes place in trees with the ♀ in a crouched position, the ♂ squatting behind her. Relationships are promiscuous (polyandrous and polygamous); an oestrous ♀ may be mounted by as many as 7 ♂♂ in one session.

REPRODUCTION AND DEVELOPMENT

Insufficient evidence for fixed mating season although copulations occur predominantly from August to November in Tanzania.⁹ In Zoos, births occur throughout the year.⁵⁷ **GESTATION PERIOD:** 225 days.⁵⁸ **BIRTH:**⁵⁹ Usually single young; labour is short and foetus is relatively small compared with both pelvic dimensions and weight of mother.¹⁵ **INFANT DEVELOPMENT:** Growth and development have been studied by Kellogg and Kellogg (1933), Schultz (1940b), Nissen and Riesen (1945, 1949), Hayes and Hayes (1951) and Gavan (1953) and Riopelle (1963); for observations on infant and juvenile behaviour in the wild, *see* Goodall (1965). **PUBERTY:** In ♀, 6–10 years (average 8.8 years); in ♂, 7–8 years.^{6, 58} **SEXUAL CYCLE:** Averages 35 days; characterized by swelling and turgescence in ano-genital region, and menstrual bleeding.

CAPTIVITY

LONGEVITY: 30–38 years. (Potential life-span has been estimated at 60 years).⁵⁸ **LONGEVITY RECORD:** *P.t. troglodytes*, 41 years (Philadelphia Zoo);⁵⁸ *P.t. schweinfurthii*, 11 years (Bronx Zoo, New York).⁶⁴ *P. troglodytes*: births in captivity are common.⁶⁵ *P. paniscus*: 2 births in World Zoos (1959–63).⁶⁵ For information on husbandry and welfare, *see* Crandall⁶⁶ and International Zoo Year Books.⁶⁵ For discussion of conservation of free-ranging chimpanzees, *see* Kortlandt (1966).

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PAPIO† Erxleben, 1777

Baboons

2 species groups: 5 species: 11 subspecies¹

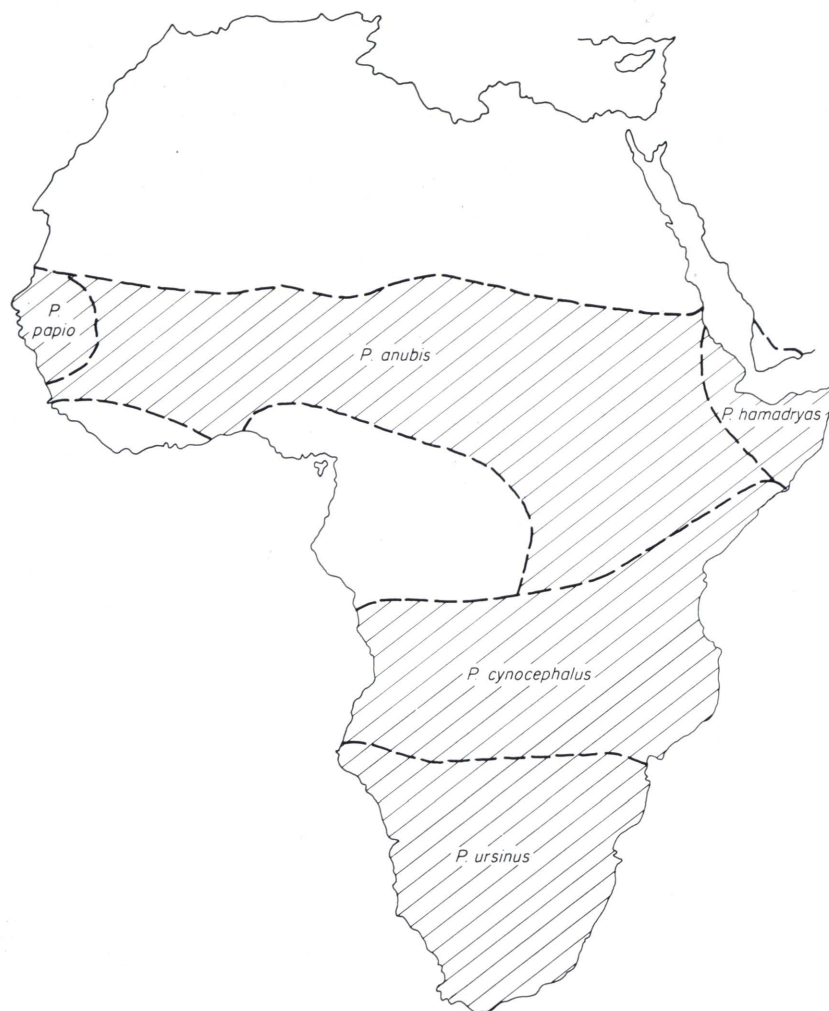
Papio cynocephalus group:

Species: <i>P. anubis</i>	Olive baboon	4 subsp.
<i>P. cynocephalus</i>	Yellow baboon	3 subsp.
<i>P. papio</i> (Type species)	Guinea baboon	0 subsp.
<i>P. ursinus</i>	Chacma baboon	4 subsp.

Papio hamadryas group:

Species: <i>P. hamadryas</i>	Sacred baboon	0 subsp.
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GEOGRAPHICAL RANGE ²⁻⁸



Africa and Asia (extreme W.). Throughout whole of sub-Saharan Africa except for southern coastal regions of Ivory Coast, Ghana and Nigeria; Congo basin, S.W. of Congo and Lualaba Rivers. Most northerly range is Tibesti plateau (*P. anubis*) and most easterly in Africa is E. Abyssinia and N. Somalia (*P. hamadryas*); this species extends into Asia to the Yemen and Aden Protectorate. Most westerly form (*P. papio*) found in Sierra Leone. The most southerly form (*P. ursinus*) extends to the Cape. All species of *Papio* replace each other geographically¹ (see range map and key to species).

The distribution of the 5 species of the genus *Papio* (after Jolly, 1965).

† See Taxonomic Notes, p. 376.



ECOLOGY

HABITAT:^{9, 10, 11} Occupy a wide range of major vegetational zones including sub-desert, savannah, Acacia thornveld, forest-savannah mosaic and rain forest. Minor habitats include rocky cliffs and gorges (*P. hamadryas*) and sea-side cliffs (*P. ursinus*). All baboons with the exception of *P. hamadryas* and some *P. ursinus*, sleep in trees. *P. cynocephalus* is the most arboreal species.^{12*} **DIET:** Omnivorous, including fruits, grasses, roots, lizards, insects; occasional meat-eating.^{10, 13, 14, 34} **ACTIVITY RHYTHM:** Diurnal. Retire to sleep from before nightfall until after dawn.

MORPHOLOGY

External Characters¹⁵

Large animals with marked sexual dimorphism in size (♂ is approx. twice the size of ♀). Largest species is *P. ursinus* and smallest *P. cynocephalus kindae*. Coat is of dense texture showing a well-developed mane in ♂ especially *P. hamadryas*¹⁶ (for Coat Colour, see Key to species). Face is long with prominent muzzle and jaws. Nares are open widely and point forwards. In *P. hamadryas*, nose is somewhat tip-tilted. Limbs are long and equal in length (particularly long in *P. cynocephalus*); tail is moderately long, generally tufted and held in characteristic U-curve (marked kink in *P. cynocephalus*). Prominent ischial callosities which are bright red in *P. papio*; they form a continuous straight transverse pad in ♂♂ being fused across midline, but are separate in ♀♀.¹⁵ Hands are rather stubby with well-marked palmar pads; fingers short and thumb relatively long.

Key to Species of *Papio*⁴⁴

- 1.a. Skin of face flesh-pink. Pelage in ♀♀ and immatures plain greyish; adult ♂♂ with copious mane of waved light-coloured hair. **HABITAT:** E. Ethiopia, northern Somalia, S.W. Arabia - - - - - *P. hamadryas*
- b. Skin of face black - - - - - *P. cynocephalus* Superspecies 2.
- 2.a. Longest hairs of back with many rings, alternating reddish and black. General colour of animal reddish, underside as back. ♂ develops mane over shoulders. **HABITAT:** Senegal to Guinea - - - - - *P. papio*
- b. Longest hairs of back with at most two light and two dark bands. General colour greyish, yellowish or brownish - - - - - 3.
- 3.a. Underside coloured as back; individual hairs brown at base, with one or two light rings, black tip. Hair of paws often black. Both sexes develop ruff round cheeks giving rounded outline to face from front. ♂ develops shoulder mane. **HABITAT:** Sierra Leone, eastwards to central Ethiopia, southwards to northern Tanzania - - - - - *P. anubis*
- b. Underside lighter than back. Hairs of cheek not forming ruff - - - - - 4.
- 4.a. Cheeks contrastingly lighter than crown, hair of paws not black. Long silky yellow hairs form fringes along back and limbs in adults. Build lanky. **HABITAT:** N. Angola to N. Mozambique, northwards to eastern Kenya, S.E. Somalia - - - - - *P. cynocephalus*
- b. Cheeks not contrastingly lighter than crown, paws often deep brown or black. Long silky *black* hairs form fringes along back and limbs in adults. Build stocky. **HABITAT:** S. Africa, northwards to southern Zambia, central Angola to S. Mozambique *P. ursinus*



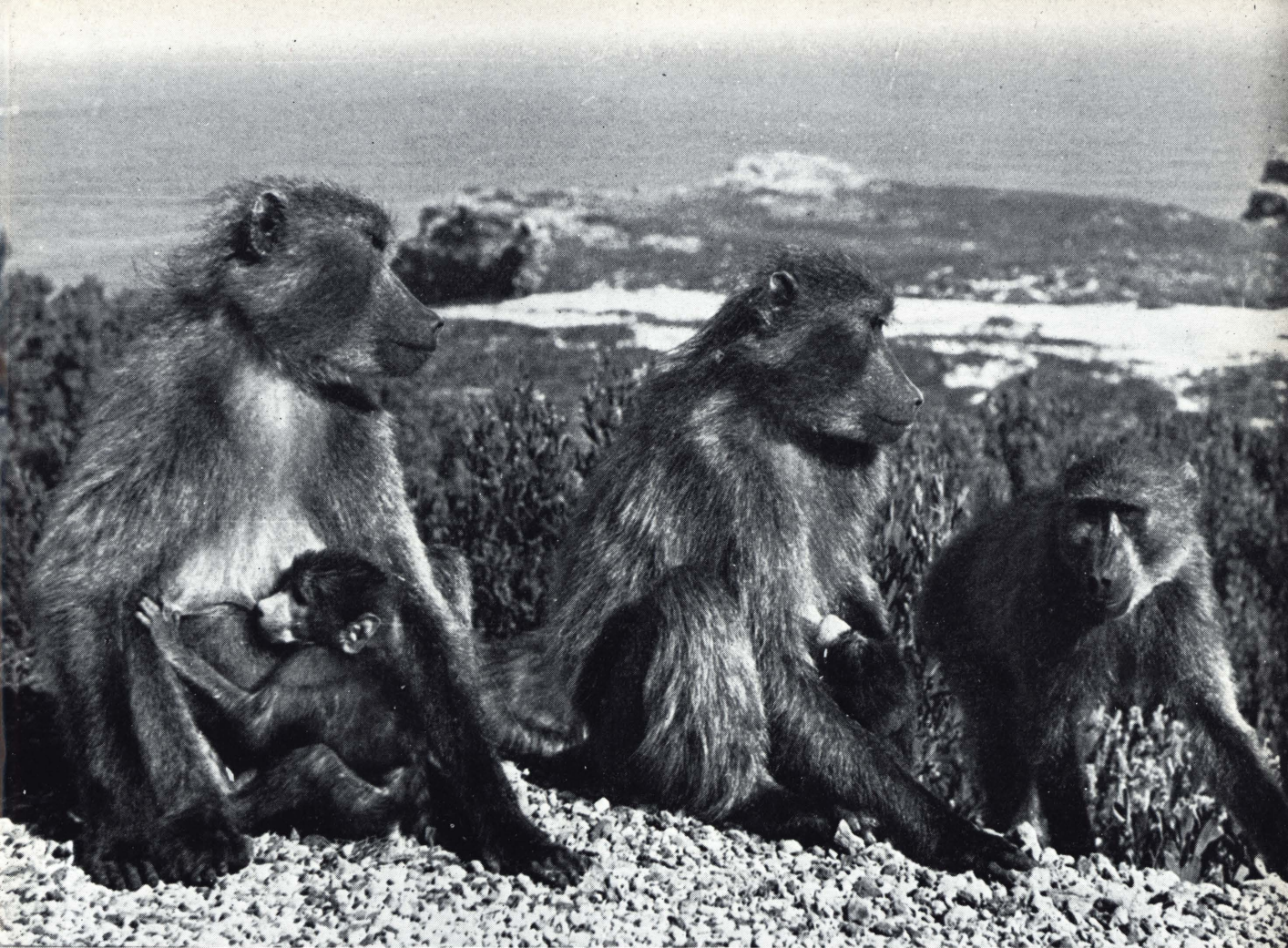


PLATE 84. *Papio ursinus*, adult ♀♀ and infants (Photos by Stephen Peet)

Left:

PLATE 83. *Papio cynocephalus*. Ischial callosities form sitting pads for night or day resting in trees (by courtesy of Sherwood L. Washburn)



Weights and Dimensions

Body weight range ¹⁷ (g)	<i>P. anubis</i>	22,000–30,000 (♂♂)	<i>P. anubis</i>	11,000–15,000 (♀♀)
Head and body length ¹⁸ (Average and Range mm)	<i>P. anubis</i>	760 (735–785) (5 ♂♂)	612 (562–660) (4 ♀♀)	
Tail length range ¹⁸ (mm) Average and Range	<i>P. anubis</i>	556 (520–600) (5 ♂♂)	462 (415–530) (4 ♀♀)	

Body weight: ♀ 50% of ♂; Head and Body length: ♀ 81% of ♂; Tail length: ♀ 83% of ♂.

Internal Characters

The special features of the anatomy of *Papio* are as follows: **SKULL**: Muzzle is elongated, in profile contour of face is flattened, nasal bones are very long. Sub-orbital depression present in paranasal region. Supra-orbital ridges continuous across midline. Calvarium relatively small and flattened; sagittal crest present. **MANDIBLE**: Mandibular torus and simian shelf well-developed and extending as far as 1st molars. Hollow on body of mandible below anterior cheek teeth. Angle of mandible obtuse and rounded. **VERTEBRAL COLUMN**:¹⁹ C.7, T.12 or 13, L.6 or 7, S.3. Slight lumbar lordosis and well-marked promontory between L.6 and S.1 (*P. hamadryas*). **FORELIMBS**: Scapula is longer and narrower than that of *Cercopithecus* and *Mandrillus*. Humerus is stout, anteriorly convex and strongly marked with muscular impressions; head points backwards and is somewhat flattened; greater tuberosity very prominent. Long, sharply defined medial lip to trochlear. Ulna has a long, backwardly tilted olecranon process. **HAND**: Metacarpals are robust with deep sesamoid gutters impressed on their heads. Trapezium bears a well-developed saddle articulation. **DENTITION**: D.F.: $\frac{2}{2} \frac{1}{1} \frac{2}{2} \frac{3}{3} = 32$. Canines exceptionally long and sharp in ♂. Premolars: PM.₁ long sloping tooth (sectorial) which is more exaggerated than in most Cercopithecinae. Molars: M.₃ largest of molar series; in this character *Papio* is more striking than other Cercopithecinae. M.₃ bears 5th cusp as in all Cercopithecidae except *Cercopithecus*.

Genetic Biology

CHROMOSOMES:^{20, 21} 2n = 42 (*P. anubis*, *P. cynocephalus*, *P. papio* and *P. hamadryas*). Karyotypes of *Papio*, *Theropithecus*, *Cercocebus* and *Macaca* have been analysed and compared by Chiarelli (1962b). **P.T.C. TASTING**:²³ 72% tasters (all species—50 specimens). *P. hamadryas* contains a higher % of non-tasters than other species. **SEROLOGICAL REACTIONS**:²⁴ High degrees of antigenic correspondence with other genera of Cercopithecinae, using immunodiffusion and electrophoretic techniques on serum and lens proteins. **HAEMOGLOBINS AND TRANSFERRINS**: See Buettner-Janusch (1963b). **BLOOD GROUPS**: For A.B.O. and Lewis blood factors, see Moor-Jankowski *et al.* (1964) and Wiener *et al.* (1966). **HAEMATOLOGY**: See Moor-Jankowski *et al.* (1965).





BEHAVIOUR

Locomotor Behaviour

AUTHORS' CLASSIFICATION: Quadrupedalism. Forelimb stance is digitigrade. Baboons move freely on the ground and in trees where at least 30% time is spent, except for *P. hamadryas* which is much less arboreal. Agile in climbing cliffs and rocks (e.g. *P. ursinus*). Capable of facultative bipedalism particularly during play. LIMB PROPORTIONS: Hindlimb very slightly longer than forelimb; radius longer than humerus giving a high Brachial Index. For Indices, see Part III, p. 395.

Hand Function

Fingers short and thumb relatively long and fully opposable; index finger used with thumb independently of other digits. Precision grip employed, e.g. during grass-plucking activity that is part of feeding repertoire. HAND PROPORTIONS: For Indices, see Part III, p. 402.

Resting Posture

Frequently sleep sitting upright on slender branches, bearing weight on ischial callosities.²⁶ Sitting posture adopted during day when resting and feeding, etc.

Social Behaviour

Evidence is accumulating that social behaviour is subject to a great deal of inter- and even intra-specific variation which appears to be closely related to the nature of habitat; recent evidence indicates, for instance, that forest-living troops of *P. anubis* in southern Uganda show a much looser social organization than populations of the same species living in open sparsely wooded country.³⁴ The following description is an abstract of a number of field studies, referring to *P. anubis*, *P. cynocephalus* and *P. ursinus*, to which reference should be made.²⁷⁻³⁴ The social structure of the sacred baboon (*P. hamadryas*), being apparently unique among true baboons, is described separately. Troop structure consists of adults, subadults, juveniles and infants of both sexes. ADULT SEX RATIO (range): 1♂ : 4♀♀ to 1♂ : 12♀♀. Group size varies from 8-200, commonly 40-80. Dominance hierarchies of both sexes are apparent and stable; role of adult ♂♂ is to lead troop, prevent intra-group fighting, protect troop from predators, protect young and inseminate ♀♀. In defensive formation, subdominant and sub-adult ♂♂ are located on periphery of group where high selection pressure on survival operates; dominant males alongside females with infants. Home range has a maximum of 15 sq miles and overlaps that of other troops; core areas, exclusive to troop, include feeding and sleeping trees and/or rocks. Inter-troop relations are generally amicable; little fighting observed in or outside troop though tension may be high. Social gestures include "presentation" of sexual area by lower animal towards one higher in social scale. Mock "mounting" by dominant animal may follow. Grooming is an important source of group stability and is freely indulged in, particularly as a prelude to, or interlude in, sexual relationships; it also occurs between females and is particularly centred on mothers with newborn infants. Play is an important activity of juveniles. Play group activity is thought to set patterns of adult social structure. VOCALIZATION:^{35, 36} Principal vocalization is by a series of grunting calls of varying length but other calls include a loud bark associated with alarm and a high-pitched shrieking associated with fear. SOCIAL ORGANIZATION OF *P. hamadryas*:^{33, 37, 38, 39} SOCIAL GROUP: One-male group is characteristic in captivity and in

PLATE 86. *Papio hamadryas*. Feeding party (above) splits into component one-male groups (below) (by courtesy of Hans Kummer and F. Kurt)



PLATE 87. *Papio ursinus*, black infant, about 6 weeks old (by courtesy of C. K. Brain)

wild populations studied so far; harem consists of a single male and 1-4 or more females, plus offspring. One-male groups foregather at night at sleeping cliffs. This grouping in *P. hamadryas* is also observed in captivity.³⁹ Male enforces following-reaction of females by means of bite in the nape of the neck (see Simonds (1965): neck-chewing by ♂ *Macaca radiata* establishes dominance among males).

Sexual Behaviour

Sexual system of *P. cynocephalus* group is promiscuous, more or less based on dominance relationships.¹⁴ Exclusive copulation by dominant ♂ takes place only when sexual swelling of ♀ is maximal; females may copulate with subdominant males prior to this. Consort-pairing

with dominant ♂ lasts for 1–3 days. Peak sexual activity, with multiple copulations, occurs early in morning in groups studied (*P. anubis*, *P. cynocephalus*, *P. ursinus*); copulations are brief, consisting of 5–10 pelvic thrusts but intervals between mountings vary considerably between species; characteristically female runs a short way from male after copulation.³⁶

REPRODUCTION AND DEVELOPMENT

Births take place throughout the year but show a peak October–December in Kenya,³⁶ Transvaal⁷ and in captivity (London).⁴⁰ GESTATION PERIOD: 170 days (Range: 154–183).⁴¹ MENSTRUATION: Length of cycle is approx. 35 days. Ovulation at approx. 19 days. LACTATION: 5–8 months.^{34, 42*} COLOUR CHANGE OF INFANT: Infant has black hair at birth and a pink face; face darkens at 4 months and coat changes colour to grey or brown; adult pelage and face colour at 10–12 months. PUBERTY: ♀ 3½–4 years; ♂ 4–6 years.

CAPTIVITY

LONGEVITY RECORD:⁴³ *P. cynocephalus*, 28 years 8 months, New York, Bronx Zoo. *P. hamadryas*, 29 years 10 months, Calgary Zoo, Canada. Breed freely in captivity. Can be kept without much difficulty but, if in colonies, then intelligent consideration for natural social grouping is essential for well-being, survival and breeding success.⁴⁷ LABORATORY USE: See symposium (Vagtborg, 1965) on the baboon as an experimental animal.

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- Moor-Jankowski, J. *et al.* (1965)

1 species: 2 subspecies¹*Pongo pygmaeus pygmaeus*

Bornean orang

Pongo pygmaeus abelii

Sumatran orang

GEOGRAPHICAL RANGE ²⁻⁵

Sumatra and Borneo. Probable range in N. Sumatra is Atjeh, N. of the Wampoe R. Centres of population in 1938 said to be along the Simpang-Kanan and the Peureulak Rivers and in forested regions of E. coast between Menlaboh and Singkel. In North Borneo (Sabah, Malaysia), oranges are found in lowland primary forest particularly in the Sandakan district. In Sarawak the diminishing orang populations are found in the forests of W. Sarawak between the Sadong and the Butang Lupar Rivers. Isolated pockets reported (1961) S. of Rajang and Balek Rivers, and around the headwaters of Balui and Baram Rivers. Distribution in Indonesian Borneo (Kalimantan) is not known.

ECOLOGY

HABITAT:³⁻⁶ Arboreal. Tropical rain forest. Peatswamp and Dipterocarp forest in Sarawak; Dipterocarp in Sabah (N. Borneo). In peatswamp forest, open canopy trees reach 120-150 ft (37-46 m); ground cover is absent and forest floor usually swampy. Orangs are found at all levels feeding among smaller branches.* Night nests in closed canopy 20-80 ft (6-24 m) above ground.^{4, 6} DIET: Predominantly frugivorous; (Durian, rambutans, etc. Durian "season": August-December); also leaves, bark and birds' eggs.* See Schaller (1961) for food list. PREDATORS: Man, indirectly, through reduction of forests for agriculture and, directly, for sale to zoos. No other known predators. ACTIVITY RHYTHM: Diurnal.

MORPHOLOGY

External Characters

Large size with marked sexual dimorphism: Sumatran forms probably larger than Bornean.⁷ Coat is rather coarse and long especially over shoulders and arms (but see Hill, 1938b). Colour in various shades of reddish-brown which becomes darker (purplish) with age. Sumatran orang is generally lighter-coloured than Bornean variety. Face is bare except for orange beard; hairy skin is bluish-black in colour and somewhat papillated. Some adult ♂♂ develop enormous cheek flanges of fat and fibrous tissue which are placed at the sides of the face like blinkers. A large dependent gular pouch is a prominent feature of adult ♂♂. Ears are small and adpressed. Face is somewhat concave ("dished"), and markedly prognathic in adults. The arms are extremely long, the hands broad and long and the thumb very small. The legs are relatively short. The foot which, at rest, is held in a curled position has long toes and a short hallux.





PLATE 92. *Pongo pygmaeus* in Sarawak, juvenile (by courtesy of Barbara Harrison)

PLATE 91. *Pongo pygmaeus*, young adult ♂ (by courtesy of Doris M. Sorby)

Weights and Dimensions^{8, 9}

	♂	♀	♀ in % of ♂
<i>Bornean Orang:</i>			
Mean body weight (kg)	189* (4♂♂)	81* (6♀♀)	43
Mean height (mm)	1370 (3♂♂)	1150 (4♀♀)	84
Mean head and body length (mm)	965 (3♂♂)	785 (6♀♀)	81
Arm span range (mm)	2150–2400		
<i>Sumatran Orang:</i>			
Mean body weight (kg)	69 (4♂♂)	37 (5♀♀)	54
Mean height (mm)	1364 (4♂♂)	1148 (3♀♀)	83.4
Mean head and body length (mm)	944 (4♂♂)	768 (5♀♀)	81.3

Note that sexual dimorphism is more apparent in weight than in body dimensions. Hill (1938) describes a single specimen of Sumatran ♂ as having a stature of 1581 mm.

* Discrepancy between weights of Bornean and Sumatran forms in spite of similarity of body size is noted with dubiety, and is probably due to a miscalculation by Lyon (1911) of the collector's figures for Bornean specimens.

Internal Characters

For details of anatomy, *see* Fick (1895), Milne-Edwards (1895), Hartmann (1885), Owen (1831, etc.), Temminck (1841), Sonntag (1924), Schultz (1930, 1941b), and Hill (1938b). The following adult characters are selected principally for their known functional importance or their value for identification. **SKULL:** The skull is domed and, in 7 out of 10 adult ♂♂, bears a sagittal crest which may be as much as 12 mm high; a nuchal crest is present in all. The orbits are usually elliptical with the longest axis vertical and the inter-orbital distance is less than in *Pan* and *Gorilla*; supra-orbital crests are not confluent. The facial skeleton is prognathous, the profile being straight or slightly concave¹⁸ (simognathic condition). The mandible is massive with a broad ascending ramus and simian shelf. On the base, the foramen magnum is placed far back, the glenoid cavities are shallow, and the mastoid process is not usually well-developed. **CRANIAL CAPACITY:**¹⁹ 405–540 cc (11♂♂): 320–400 cc (9♀♀)—*see also* Selenka (1898). **VERTEBRAL COLUMN:**¹⁶ Commonest formula: C.7, T.12, L.4, S.5 or 6. **RIBS:** 12 pairs. **UPPER LIMB:** Scapula shows the characteristic cranio-caudal elongation of brachiating apes²¹ and is sited on back of thorax. Humerus has a supra-trochlear foramen present in 80% ♂♂ and ♀♀. Radius is strongly curved; ulnar styloid does not abut against proximal carpal row even in 90° forced adduction²² (cf. *Pan* and *Gorilla*). **CARPUS:** Os centrale usually separate but shows tendency to fusion in old age. Pollex is relatively shorter than in other Pongidae but thenar muscles are remarkably specialized.²³ Metacarpals and phalanges are extremely bowed. **DIGITAL FORMULA:**⁷ 3.4.5.2.1. **LOWER LIMB:** Relatively short compared to trunk height and upper limb length (*see* Limb Proportions). **PELVIS:** Marked expansion of ilium as in *Pan* and *Gorilla*. **FEMUR:** Fossa for ligamentum teres frequently absent. **FOOT:** Hallux is relatively the shortest among all primates;²⁴ distal phalanx 5th digit absent in 60%¹⁷ when nail is also absent (*see also* Lyon, 1908a, 1911; Tuttle and Rogers, 1966). Flexor hallucis longus absent or rudimentary.²⁵ There appears to be a higher frequency of absence in Sumatran Orang (*P. p. abelii*).^{7, 9} **DENTITION:** D.F.: $\frac{2}{2} \frac{1}{2} \frac{2}{2} \frac{3}{3} = 32$. The dentition shows a typical pongid pattern as described under *Pan*. The main cusps of molar teeth show secondary wrinklins of the enamel by which they can be distinguished from *Pan* and *Gorilla*. The lower 3rd molar in

Pongo is often the longest of the series. Supernumerary molars are common in the orang.²⁶ Roots of teeth are extraordinarily long. ALIMENTARY TRACT: Intestinal tract very long; stomach similar to *Pan*.²⁷ DUCTLESS GLANDS: *See* Hill (1938b). VASCULAR: Coronary arteries; *see* Chase and De Garis (1938).

Genetic Biology

CHROMOSOMES:^{29, 30} $2n=48$ (2♂♂, 2♀♀). Karyotype suggests a less close relationship between orang and man than between chimpanzee and gorilla and man. For comparative study of the karyotypes of *Pongo*, *Pan* and *Homo*, *see* Chiarelli (1962a). IMMUNOCHEMISTRY:³² Serological evidence suggests evolutionary divergence of orang from man, gorilla and chimpanzee. P.T.C. TASTING:³³ 2 tasters : 37 non-tasters. BLOOD GROUPS:³⁴ Show ABO polymorphism, "O" phenotype being absent. Polymorphic for ABH secretor status.⁵⁰ HAEMOGLOBINS: A₂ variant (2½% frequency in *Homo*) found in this genus. *See* Barnicot and Jolly (1966).

BEHAVIOUR

Locomotor Behaviour^{4, 5, 36, 37}

AUTHORS' CLASSIFICATION: Modified Brachiation. Habitat is arboreal and they are only occasionally seen on ground. Arboreal progress is cautious,^{5, 37} and includes occasional true brachiation especially by young animals;⁵ movement is by climbing, walking quadrupedally along branches or bipedally with arms holding on above. Stability depends largely on grasping power of feet.^{4, 5, 37} All observers deny regular leaping or jumping. On the ground in captivity, bipedalism is commonly adopted;^{36, 38} normal ground gait is quadrupedal, weight being borne by the clenched fists and inverted, clenched feet (cf. *Gorilla*, *Pan*); other variations of hand posture during walking are seen in captivity, such as a palmigrade posture.²² LIMB PROPORTIONS: For Indices, *see* Part III, p. 395.

Hand Function³⁹

Hand is prehensile, thumb is short but fully opposable against proximal phalanx of index digit. The power grip is exceedingly strong and adapted for grasping slender branches. Interdigital grip frequently employed for picking up small objects. Principal grip employed in locomotion is "hook-grip" (for functional terms relating to hand use, *see* Part III, p. 396). Manipulative activities include feeding, drinking, nest-building;^{5, 36} also handling and eventual destruction of mechanical objects in captivity.³⁶ No evidence of tool-using in wild state but digging sticks are used in captivity.^{36*} HAND PROPORTIONS: *See* Part III, p. 402, for Indices.

Resting Behaviour

Nesting behaviour has been studied by Schaller (1961), Davenport (1967) and Harrisson (1960). Nests are of simple construction and do not involve interweaving or knotting. New nests are constructed every night; ground nests are not seen. Animals do not defaecate in nests⁵ (cf. *Gorilla*). Night-sleep may exceed 12 hours and frequent periods of rest, somnolence or sleep are observed during day.⁵

Social Behaviour

Reports on behaviour in wild populations are relatively few: *see* Schaller (1961), Davenport (1967) and Harrisson (1960). Ecological surveys have been carried out by Carpenter (1938), Yoshiba (1964) and Stott and Selsor (1961a). For general captivity studies, *see* Yerkes and



PLATE 93. *Pongo pygmaeus*. Hand of adult ♂ in brachiating posture

Yerkes (1929) and Harrison (1960). RANGE AND TERRITORIALITY: Unknown. GROUP SIZE:^{4, 5} Habitually 2, 3 or 4; lone ♂♂ common. GROUP COMPOSITION: (i) pairs with or without infant; (ii) ♀ with infant or juvenile; (iii) 2 or 3 subadults. POPULATION DENSITY: Sarawak:⁴ 1 per 2 sq mile (5 sq km): N. Borneo:⁶ 1 per 1 sq mile (2.5 sq km) to 1 per 2 sq miles (5 sq km). Sumatra (in 1938): two or three per 10 sq miles (25 sq km). INTRA-GROUP BEHAVIOUR: No information. VOCALIZATION:*. Orangs are silent animals with apparently a small repertoire of calls. AGONISTIC BEHAVIOUR: Throwing or dropping of branches in relation to observer reported by many workers.^{4, 5, 42, 43} SEXUAL BEHAVIOUR: Copulation is *more hominum*.⁴⁴

REPRODUCTION AND DEVELOPMENT

MENSTRUAL CYCLE: 29 days; characterized by slight menstrual flow lasting 3–4 days; periodic sexual swelling absent. GESTATION: 275 days;⁴⁵ genital swelling occurs during pregnancy⁴⁶ and mammae become prominent. BIRTH WEIGHTS: 1265–1600 g (3 infants).⁴⁶

CAPTIVITY

Births in captivity are now quite common, e.g. between 1959–63, 33 orangs were born in world zoos;⁴⁷ until 1928 (Berlin Zoo and Philadelphia Zoo) no births had been recorded.⁴⁸

LONGEVITY IN CAPTIVITY: Between 1930–1960, average life-span in London Zoo was approximately 10 years;⁴⁷ the record longevity during this period was 24 years 6 months.

LONGEVITY RECORD⁴⁹ (up to 1962): 31 years 8 months—Philadelphia Zoo.

CONSERVATION ²

Up until June, 1964, the estimated number of free-ranging orangs totalled 3800, distributed in the following manner: North Borneo (Sabah, Malaysia) 2000; Sarawak 700; Indonesian Borneo (Kalimantan) 1000; Sumatra 100.

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PART III

Supplementary and Comparative Data

Taxonomy and Nomenclature

I. SYSTEMATIC LIST OF LIVING PRIMATES

Order **PRIMATES** Linnaeus, 1758
Suborder **PROSIMII** Illiger, 1811
Infraorder **LEMURIFORMES** Gregory,
1915

Superfamily Tupaiioidea Dobson, 1882

Family Tupaiidae Mivart, 1868

Subfamily Tupaiinae Lyon, 1913

Genus *Tupaia* Raffles, 1821

Subgenus *Tupaia* Raffles, 1821

Tupaia glis Diard, 1820 (Type species)

T. g. glis Diard, 1820

T. g. belangeri Wagner, 1841

T. g. dissimilis Ellis, 1860

T. g. chinensis Anderson, 1879

T. g. modesta Allen, 1906

T. g. concolor Bonhote, 1907

T. g. siccata Thomas, 1914

T. g. laotum Thomas, 1914

T. g. sinus Kloss, 1916

T. g. clarissa Thomas, 1917

T. g. cambodiana Kloss, 1919

T. g. olivacea Kloss, 1919

T. g. assamensis Wroughton, 1921

T. g. cochinchinensis Robinson and Kloss,
1922

T. g. annamensis Robinson and Kloss, 1922

T. g. versurae Thomas, 1922

T. g. lepcha Thomas, 1922

T. g. brunetta Thomas, 1923

T. g. kobtauensis Shamel, 1930

T. g. wilkinsoni Robinson and Kloss, 1911

T. g. ferruginea Raffles, 1821

T. g. operosa Robinson and Kloss, 1914

T. g. ultima Robinson and Kloss, 1914

T. g. longicauda Kloss, 1911

T. g. obscura Kloss, 1911

T. g. sordida Miller, 1900

T. g. pemangilis Lyon, 1911

T. g. pulonis Miller, 1903

T. g. cognata Chasen, 1940

Tupaia glis Diard (continued)

T. g. umbratilis Chasen, 1940

T. g. raviana Lyon, 1911

T. g. lacernata Thomas and Wroughton,
1909

T. g. demissa Thomas, 1904

T. g. jacki Robinson and Kloss, 1918

T. g. siaca Lyon, 1908

T. g. castanea Miller, 1903

T. g. batamana Lyon, 1907

T. g. redacta Robinson, 1916

T. g. phaeura Miller, 1902

T. g. discolor Lyon, 1906

T. g. tephrrura Miller, 1903

T. g. chrysogaster Miller, 1903

T. g. siberu Chasen and Kloss, 1927

T. g. chrysomalla Miller, 1900

T. g. riabus Lyon, 1913

T. g. anambae Lyon, 1913

T. g. hypobrysa Thomas, 1895

T. g. longipes Thomas, 1893

T. g. salatana Lyon, 1913

Tupaia gracilis Thomas, 1893

T. g. gracilis Thomas, 1893

T. g. inflata Lyon, 1906

T. g. edarata Lyon, 1913

Tupaia javanica Horsfield, 1822

Tupaia minor Günther, 1876

T. m. minor Günther, 1876

T. m. malaccana Anderson, 1879

T. m. sincipis Lyon, 1911

T. m. caedis Chasen and Kloss, 1931

T. m. humeralis Robinson and Kloss, 1919

Tupaia montana Thomas, 1892

T. m. montana Thomas, 1892

T. m. baluensis Lyon, 1913

Tupaia muelleri Kohlbrugge, 1896

Tupaia nicobarica Zelebor, 1869

T. n. nicobarica Zelebor, 1869

T. n. surda Miller, 1902

Tupaia palawanensis Thomas, 1894

T. p. palawanensis Thomas, 1894

T. p. ceylonis Miller, 1910

T. p. moellendorffi Matschie, 1898

T. p. busuanga Sanborn, 1952

Tupaia picta Thomas, 1892

T. p. picta Thomas, 1892

T. p. fuscior Medway, 1965

Tupaia splendidula Gray, 1865

T. s. splendidula Gray, 1865

T. s. lucida Thomas and Hartert, 1895

T. s. natunae Lyon, 1911

T. s. carinatae Miller, 1906

Subgenus *Lyonogale* Conisbee, 1953

Tupaia tana Raffles, 1821 (Type species)

T. t. tana Raffles, 1821

T. t. speciosa Wagner, 1840

T. t. besara Lyon, 1913

T. t. nitida Chasen, 1933

T. t. utara Lyon, 1913

T. t. chrysura Günther, 1876

T. t. paitana Lyon, 1913

T. t. banguei Chasen and Kloss, 1931

T. t. cervicalis Miller, 1903

T. t. masae Lyon, 1913

T. t. tuancus Lyon, 1913

T. t. lingae Lyon, 1913

T. t. sirhassenensis Miller, 1901

T. t. bunoe Miller, 1900

T. t. kelabit Davis, 1958

T. t. kretami Davis, 1962

Tupaia dorsalis Schlegel, 1857

Genus *Anathana* Lyon, 1913

Anathana ellioti Waterhouse, 1850

A. e. ellioti Waterhouse, 1850

A. e. wroughtoni Lyon, 1913

A. e. pallida Lyon, 1913

Genus *Urogale* Mearns, 1905

Urogale everetti Thomas, 1892

Genus *Dendrogale* Gray, 1848

Dendrogale murina Schlegel and Müller, 1844

(Type species)

Dendrogale melanura Thomas, 1892

D. m. melanura Thomas, 1892

D. m. baluensis Lyon, 1913

Subfamily Ptilocercinae Lyon, 1913

Genus *Ptilocercus* Gray, 1848

Ptilocercus lowii Gray, 1848

Pt. l. lowii Gray, 1848

Pt. l. continentis Thomas, 1910

Superfamily Lemuroidea Mivart, 1864

Family Lemuridae Gray, 1821

Subfamily Lemurinae Mivart, 1864

Genus *Lemur* Linnaeus, 1758

Lemur catta Linnaeus, 1758 (Type species)

Lemur variegatus Kerr, 1792

L. v. variegatus Kerr, 1792

L. v. subcinctus A. Smith, 1833

L. v. ruber E. Geoffroy, 1812

Lemur macaco Linnaeus, 1766

L. m. macaco Linnaeus, 1766

L. m. albifrons E. Geoffroy, 1796

L. m. collaris E. Geoffroy, 1812

L. m. flavifrons Gray, 1867

L. m. fulvus E. Geoffroy, 1812

L. m. mayottensis Schlegel, 1886

L. m. rufus Audebert, 1800

L. m. sanfordi Archbold, 1932

Lemur mongoz Linnaeus, 1766

L. m. mongoz Linnaeus, 1766

L. m. coronatus Gray, 1842

Lemur rubriventer I. Geoffroy, 1850

Genus *Hapalemur* I. Geoffroy, 1851

Hapalemur griseus Link, 1795 (Type species)

H. g. griseus Link, 1795

H. g. olivaceus I. Geoffroy, 1851

Hapalemur simus Gray, 1870

Genus *Lepilemur* I. Geoffroy, 1851

Lepilemur mustelinus I. Geoffroy, 1851

L. m. mustelinus I. Geoffroy, 1851

L. m. microdon Forsyth Major, 1894

L. m. ruficaudatus Grandidier, 1867

L. m. leucopus Forsyth Major, 1894

L. m. dorsalis Gray, 1870

Subfamily Cheirogaleinae Gregory, 1915

Genus *Cheirogaleus* E. Geoffroy, 1812

Cheirogaleus major E. Geoffroy, 1812 (Type species)

Ch. m. major E. Geoffroy, 1812

Ch. m. crossleyi Grandidier, 1870

Cheirogaleus medius E. Geoffroy, 1812

Cheirogaleus trichotis Günther, 1875

Genus *Microcebus* E. Geoffroy, 1828

Microcebus murinus Miller, 1777 (Type species)

M. m. murinus Miller, 1777

M. m. smithii Gray, 1842

Microcebus coquereli Grandidier, 1867

Genus *Phaner* Gray, 1870

Phaner furcifer Blainville, 1841

Family Indriidae Burnett, 1828

Genus *Indri* E. Geoffroy and G. Cuvier, 1795

Indri indri Gmelin, 1788

Genus *Avahi* Jourdan, 1834

Avahi laniger Gmelin, 1788

A. l. laniger Gmelin, 1788

A. l. occidentalis Lorenz, 1898

Genus *Propithecus* Bennett, 1832

Propithecus diadema Bennett, 1832 (Type species)

P. d. diadema Bennett, 1832

P. d. candidus Grandidier, 1871

P. d. edwardsi Grandidier, 1871

P. d. holomelas Günther, 1875

P. d. perrieri Lavauden, 1931

Propithecus verreauxi Grandidier, 1867

P. v. verreauxi Grandidier, 1867

P. v. coquereli Milne-Edwards, 1867

P. v. coronatus Milne-Edwards, 1871

P. v. deckenii Peters, 1870

P. v. majori Rothschild, 1894

Superfamily Daubentonioidea Gill, 1872

Family Daubentoniidae Gray, 1870

Genus *Daubentonia* E. Geoffroy, 1795

Daubentonia madagascariensis Gmelin, 1788

Infraorder **LORISIFORMES** Gregory, 1915

Family Lorisidae Gregory, 1915

Subfamily Lorisinae Flower and Lydekker, 1891

Genus *Loris* E. Geoffroy, 1796

Loris tardigradus Linnaeus, 1758

L. t. tardigradus Linnaeus, 1758

L. t. grandis Hill and Phillips, 1932

L. t. lydekkerianus Cabrera, 1908

L. t. malabaricus Wroughton, 1917

L. t. nordicus Hill, 1933

L. t. nycticeboides Hill, 1942

Genus *Nycticebus* E. Geoffroy, 1812

Nycticebus coucang Boddaert, 1785 (Type species)

N. c. coucang Boddaert, 1785

N. c. bengalensis Fischer, 1804

N. c. tenasserimensis Elliot, 1913

N. c. insularis Robinson, 1917

N. c. hilleri Stone and Rehn, 1902

N. c. bancanus Lyon, 1906

N. c. borneanus Lyon, 1906

N. c. natunae Stone and Rehn, 1902

N. c. javanicus E. Geoffroy, 1812

Nycticebus pygmaeus Bonhote, 1907

Genus *Arctocebus* Gray, 1863

Arctocebus calabarensis J. A. Smith, 1860

A. c. calabarensis J. A. Smith, 1860

A. c. aureus de Winton, 1902

Genus *Perodicticus* Bennett, 1831

Perodicticus potto Müller, 1766

P. p. potto Müller, 1766

P. p. edwardsi Bouvier, 1879

P. p. faustus Thomas, 1910

P. p. ibeanus Thomas, 1910

P. p. juju Thomas, 1910

Subfamily Galaginae Mivart, 1864

Genus *Galago* E. Geoffroy, 1796

Subgenus *Galago* E. Geoffroy, 1796

Galago senegalensis E. Geoffroy, 1796 (Type species)

G. s. senegalensis E. Geoffroy, 1796

Galago senegalensis E. Geoffroy (continued)

- G. s. albipes* Dollman, 1909
G. s. braccatus Elliot, 1907
G. s. dunni Dollman, 1910
G. s. gallarum Thomas, 1901
G. s. granti Thomas and Wroughton, 1907
G. s. moholi A. Smith, 1836
G. s. sotikae Hollister, 1920
G. s. xanzibaricus Matschie, 1893

Galago crassicaudatus E. Geoffroy, 1812

- G. c. crassicaudatus* E. Geoffroy, 1812
G. c. agisymbanus Coquerel, 1859
G. c. argentatus Lönnerberg, 1913
G. c. garnettii Ogilby, 1838
G. c. kikuyuensis Lönnerberg, 1912
G. c. lasiotis Peters, 1876
G. c. loennbergi Schwarz, 1930
G. c. monteiri Gray, 1863
G. c. panganiensis Matschie, 1906
G. c. umbrosus Thomas, 1917

Galago alleni Waterhouse, 1837Subgenus *Euoticus* Gray, 1863*Galago elegantulus* Le Conte, 1857 (Type species)

- G. e. elegantulus* Le Conte, 1857
G. e. pallidus Gray, 1863

Galago inustus Schwarz, 1930Subgenus *Galagoides* A. Smith, 1833*Galago demidovii* Fischer, 1806

- G. d. demidovii* Fischer, 1806
G. d. anomurus Pousargues, 1893
G. d. orinus Lawrence and Washburn, 1936
G. d. phasma Cabrera and Ruxton, 1926
G. d. poensis Thomas, 1904
G. d. murinus Murray, 1859
G. d. thomasi Elliot, 1907

Infraorder **TARSIIFORMES** Gregory, 1915

Family Tarsiidae Gill, 1872

Genus *Tarsius* Storr, 1780*Tarsius spectrum* Pallas, 1779 (Type species)

- T. s. spectrum* Pallas, 1779
T. s. sangirensis Meyer, 1897

Tarsius spectrum Pallas (continued)

- T. s. dentatus* Miller and Hollister, 1921
T. s. pumilis Miller and Hollister, 1921
T. s. pelengensis Sody, 1949
Tarsius bancanus Horsfield, 1821
T. b. bancanus Horsfield, 1821
T. b. saltator Elliot, 1910
T. b. borneanus Elliot, 1910
T. b. natunensis Chasen, 1940
Tarsius syrichta Linnaeus, 1758
T. s. syrichta Linnaeus, 1758
T. s. fraterculus Miller, 1910
T. s. carbonarius Heude, 1898

Suborder **ANTHROPOIDEA** Mivart, 1864

Superfamily Ceboidea Simpson, 1931

Family Callitrichidae Thomas, 1903

Subfamily Callitrichinae Thomas, 1903

Genus *Callithrix* Erxleben, 1777*Callithrix jacchus* Linnaeus, 1758 (Type species)*Callithrix argentata* Linnaeus, 1766

- C. a. argentata* Linnaeus, 1766
C. a. emiliae Thomas, 1920
C. a. leucippe Thomas, 1922
C. a. melanura E. Geoffroy, 1812
Callithrix aurita E. Geoffroy, 1812
C. a. aurita E. Geoffroy, 1812
C. a. coelestis Ribiero, 1924

Callithrix flaviceps Thomas, 1903*Callithrix geoffroyi* Humboldt, 1812*Callithrix penicillata* E. Geoffroy, 1812

- C. p. penicillata* E. Geoffroy, 1812
C. p. jordani Thomas, 1904

Callithrix humeralifer E. Geoffroy, 1812*Callithrix chrysolenca* Wagner, 1842Genus *Cebuella* Gray, 1866*Cebuella pygmaea* Spix, 1823

- C. p. pygmaea* Spix, 1823
C. p. niveiventris Lönnerberg, 1940

Genus *Saguinus* Hoffmannsegg, 1807Subgenus *Saguinus* Hoffmannsegg, 1807*Saguinus tamarin* Link, 1795 (Type species)

Saguinus devillei I. Geoffroy, 1851
Saguinus fuscicollis Spix, 1823
Saguinus fuscus Lesson, 1840
Saguinus graellsii Espada, 1870
Saguinus illigeri Pucheran, 1845
Saguinus imperator Goeldi, 1907
S. i. imperator Goeldi, 1907
S. i. subgriseus Lönnberg, 1940
Saguinus melanoleucus Ribiero, 1912
Saguinus midas Linnaeus, 1758
Saguinus labiatus E. Geoffroy, 1812
S. l. labiatus, E. Geoffroy, 1812
S. l. griseovortex Goeldi, 1907
Saguinus mystax Spix, 1823
Saguinus pileatus I. Geoffroy and Deville, 1848
Saguinus pluto Lönnberg, 1926
Saguinus weddelli Deville, 1849
Saguinus nigricollis Spix, 1823
Saguinus lagonotus Espada, 1870

Subgenus *Oedipomidas* Reichenbach, 1862
Saguinus oedipus Linnaeus, 1758 (Type species)
Saguinus geoffroyi Pucheran, 1845

Subgenus *Marikina* Lesson, 1840
Saguinus bicolor Spix, 1823 (Type species)
Saguinus martinsi Thomas, 1912
Saguinus leucopus Günther, 1876
Saguinus inustus Schwarz, 1951

Genus *Leontideus* Cabrera, 1956
Leontideus rosalia Linnaeus, 1766 (Type species)
Leontideus chrysomelas Kuhl, 1820
Leontideus chrysopygus Mikan, 1823

Subfamily Callimiconinae Thomas, 1913
Genus *Callimico* Ribiero, 1911
Callimico goeldii Thomas, 1904

Family Cebidae Swainson, 1835
Subfamily Aotinae Elliot, 1913
Genus *Aotus* Illiger, 1811
Aotus trivirgatus Humboldt, 1812
A. t. trivirgatus Humboldt, 1812

Aotus trivirgatus Humboldt (continued)
A. t. boliviensis Elliot, 1907
A. t. griseimembra Elliot, 1912
A. t. lemurinus I. Geoffroy, 1843
A. t. microdon Dollman, 1909
A. t. nigriceps Dollman, 1909
A. t. roberti Dollman, 1909
A. t. bipunctatus Bole, 1937
A. t. azarae Humboldt, 1812

Genus *Callicebus* Thomas, 1903
Callicebus personatus E. Geoffroy, 1812 (Type species)
C. p. personatus E. Geoffroy, 1812
C. p. brunello Thomas, 1913
C. p. nigrifrons Spix, 1823
C. p. melanocheir Kuhl, 1820
Callicebus moloch Hoffmannsegg, 1807
C. m. moloch Hoffmannsegg, 1807
C. m. donacophilus d'Orbigny, 1836
C. m. hoffmannsi Thomas 1908
C. m. brunneus Wagner, 1842
C. m. cupreus Spix, 1823
C. m. discolor I. Geoffroy and Deville, 1848
C. m. ornatus Gray, 1866
Callicebus torquatus Hoffmannsegg, 1807
C. t. torquatus Hoffmannsegg, 1807
C. t. lugens Humboldt, 1812
C. t. medemi Hershkovitz, 1963

Subfamily Pitheciinae Mivart, 1865
Genus *Pithecia* Desmarest, 1804
Pithecia pithecia Linnaeus, 1766 (Type species)
Pithecia monachus E. Geoffroy, 1812
P. m. monachus E. Geoffroy, 1812
P. m. capillamentosa Spix, 1823

Genus *Chiropotes* Lesson, 1840
Chiropotes satanas Hoffmannsegg, 1807 (Type species)
Ch. s. satanas Hoffmannsegg, 1807
Ch. s. chiropotes Humboldt, 1812
Chiropotes albinasus I. Geoffroy and Deville, 1848

Genus *Cacajao* Lesson, 1840

Cacajao melanocephalus Humboldt, 1812 (Type species)

Cacajao calvus I. Geoffroy, 1847

Cacajao rubicundus I. Geoffroy and Deville, 1848

C. r. rubicundus I. Geoffroy and Deville, 1848

C. r. ucayalii Thomas, 1928

Subfamily Alouattinae Elliot, 1904

Genus *Alouatta* Lacépède, 1799

Alouatta belzebul Linnaeus, 1766 (Type species)

A. b. belzebul Linnaeus, 1766

A. b. discolor Spix, 1823

A. b. mexicana Hagmann, 1908

A. b. nigerrima Lönnberg, 1941

A. b. ululata Elliot, 1912

Alouatta villosa Gray, 1845

A. v. villosa Gray, 1845

A. v. aequatorialis Festa, 1903

A. v. coibensis Thomas, 1902

A. v. luctuosa Lawrence, 1933

A. v. mexicana Merriam, 1902

A. v. palliata Gray, 1849

A. v. pigra Lawrence, 1933

A. v. trabeata Lawrence, 1933

Alouatta seniculus Linnaeus, 1766

A. s. seniculus Linnaeus, 1766

A. s. sara Elliot, 1910

A. s. straminea Humboldt, 1812

A. s. arctoidea Cabrera, 1940

A. s. insulanus Elliot, 1910

Alouatta caraya Humboldt, 1812

Alouatta fusca E. Geoffroy, 1812

A. f. fusca E. Geoffroy, 1812

A. f. beniensis Lönnberg, 1941

A. f. clamitans Cabrera, 1940

Subfamily Cebinae Mivart, 1865

Genus *Cebus* Erxleben, 1777

Cebus capucinus Linnaeus, 1758 (Type species)

C. c. capucinus Linnaeus, 1758

C. c. curtus Bangs, 1905

Cebus capucinus Linnaeus (continued)

C. c. imitator Thomas, 1903

C. c. limitaneus Hollister, 1914

C. c. nigripectus Elliot, 1909

Cebus albifrons Humboldt, 1812

C. a. albifrons Humboldt, 1812

C. a. hypoleucus Humboldt, 1812

C. a. cesarae Hershkovitz, 1949

C. a. pleei Hershkovitz, 1949

C. a. versicolor Pucheran, 1845

C. a. leucocephalus Gray, 1865

C. a. adustus Hershkovitz, 1949

C. a. unicolor Spix, 1823

C. a. yuracus Hershkovitz, 1949

C. a. cuscinus Thomas, 1901

C. a. aequatorialis Allen, 1914

C. a. trinitatis von Pusch, 1941

Cebus nigrivittatus Wagner, 1848

C. n. nigrivittatus Wagner, 1848

C. n. apiculatus Elliot, 1907

C. n. brunneus Allen, 1914

C. n. castaneus I. Geoffroy, 1851

C. n. olivaceus Schomburgk, 1848

Cebus apella Linnaeus, 1758

C. a. apella Linnaeus, 1758

C. a. margaritae Hollister, 1914

C. a. macrocephalus Spix, 1823

C. a. pallidus Gray, 1865

C. a. libidinosus Spix, 1823

C. a. xanthosternus Wied, 1820

C. a. robustus Kuhl, 1820

C. a. nigrinus Goldfuss, 1809

C. a. cay Illiger, 1815

C. a. vellerosus I. Geoffroy, 1851

C. a. versutus Elliot, 1910

Genus *Saimiri* Voigt, 1831

Saimiri sciureus Linnaeus, 1758

S. s. sciureus Linnaeus, 1758

S. s. boliviensis d'Orbigny, 1834

S. s. collinsi Osgood, 1916

S. s. macrodon Elliot, 1907

S. s. nigriceps Thomas, 1902

S. s. ustus I. Geoffroy, 1844

Saimiri oerstedii Reinhardt, 1872

S. oe. oerstedii Reinhardt, 1872

S. oe. citrinellus Thomas, 1904

Subfamily Atelinae Miller, 1924

Genus *Ateles* E. Geoffroy, 1806

Ateles paniscus Linnaeus, 1758 (Type species)

A. p. paniscus Linnaeus, 1758

A. p. chamek Humboldt, 1812

Ateles belzebuth E. Geoffroy, 1806

A. b. belzebuth E. Geoffroy, 1806

A. b. hybridus I. Geoffroy, 1829

A. b. marginatus E. Geoffroy, 1809

Ateles fusciceps Gray, 1866

A. f. fusciceps Gray, 1866

A. f. robustus J. A. Allen, 1914

Ateles geoffroyi Kuhl, 1820

A. g. geoffroyi Kuhl, 1820

A. g. vellerosus Gray, 1866

A. g. yucatanensis Kellogg and Goldman, 1944

A. g. pan Schlegel, 1876

A. g. frontatus Gray, 1842

A. g. ornatus Gray, 1870

A. g. panamensis Kellogg and Goldman, 1944

A. g. azuerensis Bole, 1937

A. g. griseus Gray, 1866

Genus *Brachyteles* Spix, 1823

Brachyteles arachnoides E. Geoffroy, 1806

Genus *Lagothrix* E. Geoffroy, 1812

Lagothrix lagothricha Humboldt, 1812 (Type species)

L. l. lagothricha Humboldt, 1812

L. l. lugens Elliot, 1907

L. l. poeppigii Schinz, 1844

L. l. cana E. Geoffroy, 1812

Lagothrix flavicauda Humboldt, 1812

Superfamily Cercopithecoidea Simpson, 1931

Family Cercopithecidae Gray, 1821

Subfamily Cercopithecinae Blanford, 1888

Genus *Macaca* Lacépède, 1799

Macaca sylvana Linnaeus, 1758 (Type species)

Macaca sinica Linnaeus, 1771

M. s. sinica Linnaeus, 1771

M. s. aurifrons Pocock, 1931

M. s. opisthomelas Hill, 1942

Macaca radiata E. Geoffroy, 1812

M. r. radiata E. Geoffroy, 1812

M. r. diluta Pocock, 1931

Macaca silenus Linnaeus, 1758

Macaca nemestrina Linnaeus, 1766

M. n. nemestrina Linnaeus, 1766

M. n. leonina Blyth, 1863

M. n. blythii Pocock, 1931

M. n. pagensis Miller, 1903

Macaca fascicularis Raffles, 1821

M. f. fascicularis Raffles, 1821

M. f. aurea E. Geoffroy, 1831

M. f. umbrosa Miller, 1902

M. f. valida Elliot, 1909

M. f. atriceps Kloss, 1919

M. f. argentimembris Kloss, 1911

M. f. capitalis Elliot, 1910

M. f. laeti Elliot, 1909

M. f. pumila Miller, 1900

M. f. fusca Miller, 1903

M. f. lasiae Lyon, 1916

M. f. phaeura Miller, 1903

M. f. mordax Thomas and Wroughton, 1909

M. f. cupida Elliot, 1910

M. f. baweanana Elliot, 1910

M. f. philippinensis I. Geoffroy, 1843

M. f. mindanensis Mearns, 1905

M. f. mindora Hollister, 1913

M. f. tua Kellogg, 1944

M. f. limitis Schwarz, 1913

M. f. sublimitis Sody, 1933

Macaca mulatta Zimmerman, 1780

M. m. mulatta Zimmerman, 1780

M. m. vestita Milne-Edwards, 1892

M. m. villosa True, 1894

M. m. mcmahoni Pocock, 1932

Macaca assamensis M'Clelland, 1839

M. a. assamensis M'Clelland, 1839

M. a. pelops Hodgson, 1840

Macaca cyclopis Swinhoe, 1862

Macaca speciosa F. Cuvier, 1825

M. s. speciosa F. Cuvier, 1825

M. s. arctoides I. Geoffroy, 1831

M. s. melanota Ogilby, 1839

M. s. thibetana Milne-Edwards, 1870

Macaca fuscata Blyth, 1875

Macaca fuscata Blyth (continued)*M. f. fuscata* Blyth, 1875*M. f. yakui* Kuroda, 1941*Macaca maurus* F. Cuvier, 1823*M. m. maurus* F. Cuvier, 1823*M. m. brunnescens* Matschie, 1901*M. m. togeana* Sody, 1949*M. m. ochreata* Ogilby, 1840Genus *Cynopithecus* I. Geoffroy, 1835*Cynopithecus niger* Desmarest, 1822*C. n. niger* Desmarest, 1822*C. n. lembicus* Miller, 1931Genus *Cercocebus* E. Geoffroy, 1812*Cercocebus albigena* group:*Cercocebus albigena* Gray, 1850*C. a. albigena* Gray, 1850*C. a. johnstoni* Lydekker, 1900*C. a. zenkeri* Schwarz, 1910*Cercocebus aterrimus* Oudemans, 1890*Cercocebus torquatus* group:*Cercocebus torquatus* Kerr, 1792*Cercocebus atys* Audebert, 1797 (Type species)*C. a. atys* Audebert, 1797*C. a. lunulatus* Temminck, 1853*Cercocebus galeritus* Peters, 1879*C. g. galeritus* Peters, 1879*C. g. agilis* Rivière, 1886*C. g. chrysogaster* Lydekker, 1900Genus *Papio* Erxleben, 1777*Papio cynocephalus* group:*Papio anubis* Lesson, 1827*P. a. anubis* Lesson, 1827*P. a. tibestianus* Dekeyser and Derivot, 1960*P. a. heuglini* Matschie, 1898*P. a. neumannii* Matschie, 1897*Papio cynocephalus* Linnaeus, 1766*P. c. cynocephalus* Linnaeus, 1766*P. c. ibeanus* Thomas, 1893*P. c. kindae* Lönnberg, 1919*Papio papio* Desmarest, 1820 (Type species)*Papio ursinus* Kerr, 1792*P. u. ursinus* Kerr, 1792*P. u. orientalis* Goldblatt, 1926*Papio ursinus* Kerr (continued)*P. u. ruacana* Shortridge, 1942*P. u. griseipes* Pocock, 1911*Papio hamadryas* group:*Papio hamadryas* Linnaeus, 1758Genus *Mandrillus* Ritgen, 1824*Mandrillus sphinx* Linnaeus, 1758 (Type species)*Mandrillus leucophaeus* F. Cuvier, 1807*M. l. leucophaeus* F. Cuvier, 1807*M. l. poensis* Zukowsky, 1922Genus *Theropithecus* I. Geoffroy, 1841*Theropithecus gelada* Rüppell, 1835*Th. g. gelada* Rüppell, 1835*Th. g. obscurus* Heuglin, 1863Genus *Cercopithecus* Linnaeus, 1758Subgenus *Cercopithecus* Linnaeus, 1758*Cercopithecus aethiops* group:*Cercopithecus aethiops* Linnaeus, 1758*C. ae. aethiops* Linnaeus, 1758*C. ae. hilgerti* Neumann, 1902*C. ae. ellenbecki* Neumann, 1902*C. ae. zavattarii* de Beaux, 1943*C. ae. tantalus* Ogilby, 1841*C. ae. budgetti* Pocock, 1907*C. ae. marrensis* Thomas and Wroughton, 1923*Cercopithecus pygerythrus* F. Cuvier, 1821*C. p. pygerythrus* F. Cuvier, 1821*C. p. arenarius* Heller, 1913*C. p. centralis* Neumann, 1900*C. p. callidus* Hollister, 1912*C. p. johnstoni* Pocock, 1907*C. p. excubitor* Schwarz, 1926*C. p. nesiotes* Schwarz, 1926*C. p. rufoviridis* I. Geoffroy, 1842*C. p. whytei* Pocock, 1907*C. p. cloeti* Roberts, 1931*C. p. ngamiensis* Roberts, 1932*C. p. marjoriae* Bradfield, 1936*C. p. cynosuroides* Scopoli, 1786*Cercopithecus sabaenus* Linnaeus, 1766*Cercopithecus cephus* group:*Cercopithecus cephus* Linnaeus, 1766

- Cercopithecus cephus* Linnaeus (continued)
C. c. cephus Linnaeus, 1766
C. c. cephodes Pocock, 1907
- Cercopithecus diana* group:
Cercopithecus diana Linnaeus, 1758 (Type species)
C. d. diana Linnaeus, 1758
C. d. roloway Schreber, 1774
C. d. dryas Schwarz, 1932
- Cercopithecus lhoesti* group:
Cercopithecus lhoesti Sclater, 1898
Cercopithecus preussi Matschie, 1898
- Cercopithecus hamlyni* group:
Cercopithecus hamlyni Pocock, 1907
- Cercopithecus mitis* group:
Cercopithecus mitis Wolf, 1822
C. m. mitis Wolf, 1822
C. m. boutourlinii Giglioli, 1887
C. m. stuhlmanni Matschie, 1893
C. m. doggetti Pocock, 1907
C. m. maesi Lönnberg, 1919
C. m. kandti Matschie, 1905
C. m. schoutedeni Schwarz, 1928
C. m. opisthostictus Sclater, 1893
- Cercopithecus albogularis* Sykes, 1831
C. a. albogularis Sykes, 1831
C. a. albotorquatus Pousargues, 1896
C. a. monoides I. Geoffroy, 1841
C. a. phylax Schwarz, 1927
C. a. kibonotensis Lönnberg, 1910
C. a. kolbi Neumann, 1902
C. a. moloneyi Sclater, 1893
C. a. francescae Thomas, 1902
C. a. nyasae Schwarz, 1928
C. a. erythrarchus Peters, 1852
C. a. schwarzi Roberts, 1931
C. a. labiatus I. Geoffroy, 1841
- Cercopithecus mona* group:
Cercopithecus mona Schreber, 1774
Cercopithecus campbelli Waterhouse, 1838
C. c. campbelli Waterhouse, 1838
C. c. lowei Thomas, 1923
- Cercopithecus wolffi* Meyer, 1891
C. w. wolffi Meyer, 1891
C. w. pyrogaster Lönnberg, 1919
C. w. elegans Dubois and Matschie, 1912
- Cercopithecus denti* Thomas, 1907
- Cercopithecus pogonias* Bennett, 1833
C. p. pogonias Bennett, 1833
C. p. grayi Fraser, 1850
C. p. nigripes du Chaillu, 1860
C. p. schwarzi Schouteden, 1946
- Cercopithecus neglectus* group:
Cercopithecus neglectus Schlegel, 1876
- Cercopithecus nictitans* group:
Cercopithecus nictitans Linnaeus, 1766
C. n. nictitans Linnaeus, 1766
C. n. martini Waterhouse, 1841
C. n. stampflii Jentink, 1888
- Cercopithecus petaurista* Schreber, 1775
C. p. petaurista Schreber, 1775
C. p. buettikoferi Jentink, 1886
- Cercopithecus ascanius* Audebert, 1799
C. a. ascanius Audebert, 1799
C. a. katangae Lönnberg, 1919
C. a. whitesidei Thomas, 1909
C. a. montanus Lorenz, 1914
C. a. schmidtii Matschie, 1892
- Cercopithecus erythrotis* Waterhouse, 1838
C. e. erythrotis Waterhouse, 1838
C. e. camerunensis Hayman, 1940
C. e. sclateri Pocock, 1904
- Cercopithecus erythrogaster* Gray, 1866
- Subgenus *Miopithecus* I. Geoffroy, 1842
Cercopithecus talapoin Schreber, 1774
C. t. talapoin Schreber, 1774
C. t. ansorgei Pocock, 1907
C. t. vleeschouwersi Poll, 1940
C. t. pilettei Lönnberg, 1919
- Subgenus *Allenopithecus* Lang, 1923
Cercopithecus nigroviridis Pocock, 1907
- Genus *Erythrocebus* Trouessart, 1897
Erythrocebus patas Schreber, 1775
E. p. patas Schreber, 1775
E. p. villiersi Dekeyser, 1950
E. p. pyrronotus Hemprich and Ehrenberg, 1829
E. p. baumstarki Matschie, 1905
- Subfamily Colobinae Elliot, 1913
Genus *Presbytis* Eschscholtz, 1821



Presbytis aygula group:*Presbytis aygula* Linnaeus, 1758 (Type species)*P. a. aygula* Linnaeus, 1758*P. a. fredericae* Sody, 1930*P. a. bosei* Thomas, 1889*P. a. canicrus* Miller, 1934*P. a. nubilus* Millar, 1942*P. a. sabanus* Thomas, 1893*P. a. thomasi* Collett, 1892*P. a. margae* Hooijer, 1948*Presbytis melalophos* Raffles, 1821*P. m. melalophos* Raffles, 1821*P. m. femoralis* Martin, 1838*P. m. australis* Miller, 1913*P. m. siamensis* Müller and Schlegel, 1841*P. m. nubigena* Elliot, 1909*P. m. robinsoni* Thomas, 1910*P. m. rhionis* Miller, 1903*P. m. canus* Miller, 1906*P. m. natunae* Thomas and Hartert, 1894*P. m. catemanus* Lyon, 1908*P. m. percura* Lyon, 1908*P. m. paenulatus* Chasen, 1940*P. m. sumatranus* Müller and Schlegel, 1841*P. m. batuanus* Miller, 1903*P. m. ferrugineus* Schlegel, 1876*P. m. fluviatilis* Chasen, 1940*P. m. fuscomurinus* Elliot, 1906*P. m. chrysomelas* Müller, 1838*P. m. cruciger* Thomas, 1892*Presbytis frontatus* Müller, 1838*P. f. frontatus* Müller, 1838*P. f. nudifrons* Elliot, 1909*Presbytis rubicundus* Müller, 1838*P. r. rubicundus*, Müller, 1838*P. r. rubidus* Lyon, 1911*P. r. ignitus* Dollman, 1909*P. r. carinatae* Miller, 1906*P. r. chryseus* Davis, 1962*Presbytis entellus* group:*Presbytis entellus* Dufresne, 1797*P. e. entellus* Dufresne, 1797*P. e. schistaceus* Hodgson, 1840*P. e. hypoleucos* Blyth, 1841*P. e. dussumieri* I. Geoffroy, 1843*P. e. anchises* Blyth, 1844*P. e. priam* Blyth, 1844*Presbytis entellus* Dufresne (continued)*P. e. thersites* Blyth, 1847*P. e. lania* Elliot, 1909*P. e. achilles* Pocock, 1928*P. e. ajax* Pocock, 1928*P. e. achates* Pocock, 1928*P. e. iulus* Pocock, 1928*P. e. aeneas* Pocock, 1928*P. e. elissa* Pocock, 1928*P. e. priamellus* Pocock, 1928*Presbytis senex* group:*Presbytis senex* Erxleben, 1777*P. s. senex* Erxleben, 1777*P. s. vetulus* Erxleben, 1777*P. s. nestor* Bennett, 1833*P. s. monticola* Kelaart, 1850*P. s. harti* Deraniyagala, 1954*Presbytis johnii* Fischer, 1829*Presbytis cristatus* group:*Presbytis cristatus* Raffles, 1821*P. c. cristatus* Raffles, 1821*P. c. pyrrhus* Horsfield, 1823*P. c. sondaicus* Robinson and Kloss, 1919*P. c. kohlbruggei* Sody, 1931*P. c. ultimus* Elliot, 1910*P. c. vigilans* Miller, 1913*P. c. germaini* Milne-Edwards, 1876*P. c. atrior* Pocock, 1928*Presbytis pileatus* Blyth, 1843*P. p. pileatus* Blyth, 1843*P. p. shortridgei* Wroughton, 1915*P. p. brahma* Wroughton, 1916*P. p. durga* Wroughton, 1916*P. p. tenebricus* Hinton, 1923*Presbytis geei* Gee, 1956*Presbytis obscurus* Reid, 1837*P. o. obscurus* Reid, 1837*P. o. flavicauda* Elliot, 1910*P. o. halonifer* Cantor, 1845*P. o. carbo* Thomas and Wroughton, 1909*P. o. styx* Kloss, 1911*P. o. seimundi* Chasen, 1940*P. o. sanctorum* Elliot, 1910*Presbytis phayrei* Blyth, 1847*P. p. phayrei* Blyth, 1847*P. p. crepusculus* Elliot, 1909*P. p. shanicus* Wroughton, 1917

Presbytis phayrei Blyth (continued)*P. p. ruhei* Knottnerus-Meyer, 1933*Presbytis francoisi* Pousargues, 1898*P. f. francoisi* Pousargues, 1898*P. f. poliocephalus* Trouessart, 1911*P. f. laotum* Thomas, 1921*P. f. delacouri* Osgood, 1932*Presbytis potenziani* Bonaparte, 1856*P. p. potenziani* Bonaparte, 1856*P. p. siberu* Chasen and Kloss, 1927Genus *Rhinopithecus* Milne-Edwards, 1872*Rhinopithecus roxellanae* Milne-Edwards, 1870

(Type species)

Rh. r. roxellanae Milne-Edwards, 1870*Rh. r. bieti* Milne-Edwards, 1897*Rh. r. brelichi* Thomas, 1903*Rhinopithecus avunculus* Dollman, 1912Genus *Pygathrix* E. Geoffroy, 1812*Pygathrix nemaeus* Linnaeus, 1771*P. n. nemaeus* Linnaeus, 1771*P. n. nigripes* Milne-Edwards, 1871Genus *Nasalis* E. Geoffroy, 1812*Nasalis larvatus* Wurmbe, 1781Genus *Simias* Miller, 1903*Simias concolor* Miller, 1903*S. c. concolor* Miller, 1903*S. c. siberu* Chasen and Kloss, 1927Genus *Colobus* Illiger, 1811Subgenus *Colobus* Illiger, 1811*Colobus polykomos* Zimmerman, 1780 (Type species)*C. p. polykomos* Zimmerman, 1780*C. p. adolfifriederici* Matschie, 1914*C. p. angolensis* Sclater, 1860*C. p. cordieri* Rahm, 1959*C. p. cottoni* Lydekker, 1905*C. p. dollmani* Schwarz, 1927*C. p. palliatus* Peters, 1868*C. p. prigoginei* Verheyen, 1959*C. p. ruwenzorii* Thomas, 1901*C. p. satanas* Waterhouse, 1838*C. p. sharpei* Thomas, 1902*C. p. vellerosus* I. Geoffroy, 1834*Colobus guereza* Rüppell, 1835*C. g. guereza* Rüppell, 1835*C. g. caudatus* Thomas, 1885*C. g. dodingae* Matschie, 1913*C. g. gallarum* Neumann, 1902*C. g. kikuyuensis* Lönnberg, 1912*C. g. matschiei* Neumann, 1899*C. g. occidentalis* Rochebrune, 1886-7*C. g. percivali* Heller, 1913*C. g. poliurus* Thomas, 1901*C. g. uellensis* Matschie, 1913Subgenus *Procolobus* Rochebrune, 1886-7*Colobus verus* van Beneden, 1838Subgenus *Piliocolobus* Rochebrune, 1886-7*Colobus badius* Kerr, 1792 (Type species)*C. b. badius*, Kerr, 1792*C. b. bouvieri* Rochebrune, 1887*C. b. ellioti* Dollman, 1909*C. b. foai* Pousargues, 1899*C. b. gordonorum* Matschie, 1900*C. b. graueri* Dollman, 1909*C. b. gudoviusi* Matschie, 1914*C. b. langi* J. A. Allen, 1925*C. b. metternichi* Krumbiegel, 1942*C. b. nigrimanus* Trouessart, 1906*C. b. oustaleti* Trouessart, 1906*C. b. pennantii* Waterhouse, 1838*C. b. powelli* Matschie, 1913*C. b. preussi* Matschie, 1900*C. b. rufomitratu*s Peters, 1879*C. b. temminckii* Kuhl, 1820*C. b. tephroceles* Elliot, 1907*C. b. tholloni* Rivière, 1886*C. b. waldroni* Hayman, 1936*Colobus kirkii* Gray, 1868

Superfamily Hominoidea Simpson, 1931

Family Hylobatidae Blyth, 1875

Genus *Hylobates* Illiger, 1811*Hylobates lar* Linnaeus, 1771 (Type species)*H. l. lar* Linnaeus, 1771*H. l. longimanus* Schreber, 1775*H. l. pileatus* Gray, 1861*Hylobates moloch* Audebert, 1797-8

Hylobates moloch Audebert (continued)*H. m. moloch* Audebert, 1797-8*H. m. pongoalsoni* Sody, 1949*H. m. muelleri* Martin, 1841*H. m. albibarbis* Lyon, 1911*H. m. abbotti* Kloss, 1929*H. m. funereus* I. Geoffroy, 1850*Hylobates agilis* F. Cuvier, 1821*Hylobates hooleck* Harlan, 1834*Hylobates concolor* Harlan 1826*H. c. concolor* Harlan, 1826*H. c. hainanus* Thomas, 1892*H. c. lu* Delacour, 1951*H. c. leucogenys* Ogilby, 1840*H. c. siki* Delacour, 1951*H. c. gabriellae* Thomas, 1909*Hylobates klossii* Miller, 1903Genus *Symphalangus* Gloger, 1841*Symphalangus syndactylus* Raffles, 1821*S. s. syndactylus* Raffles, 1821*S. s. continentis* Thomas, 1908

Family Pongidae Elliot, 1913

Genus *Pongo* Lacépède, 1799*Pongo pygmaeus* Linnaeus, 1760*P. p. pygmaeus* Linnaeus, 1760*P. p. abelii* Lesson, 1827Genus *Pan* Oken, 1816*Pan troglodytes* Blumenbach, 1779 (Type species)*P. t. troglodytes* Blumenbach, 1779*P. t. verus* Schwarz, 1934*P. t. schweinfurthii* Giglioli, 1872*Pan paniscus* Schwarz, 1929Genus *Gorilla* I. Geoffroy, 1852*Gorilla gorilla* Savage and Wyman, 1847*G. g. gorilla* Savage and Wyman, 1847*G. g. beringei* Matschie, 1903*G. g. manyema* Rothschild, 1908

Family Hominidae Gray, 1825

Genus *Homo* Linnaeus, 1758*Homo sapiens* Linnaeus, 1758

2. SOME COMMON SYNONYMS

Alouatta guariba = *Alouatta fusca*
Alouatta palliata = *Alouatta villosa*
Anthropopithecus = *Pan*
Aotes = *Aotus*
Ateles = *Ateles*
Bonobo = *Pan paniscus*
Brachitanytes = *Hylobates klossii*
Brachyurus = *Cacajao*
Cebus fatuellus = *Cebus apella*
Chaeropithecus = *Papio*
Chrysothrix = *Saimiri*
Colobus abyssinicus = *Colobus guereza*
Comopithecus = *Papio hamadryas*
Cynocephalus = *Papio*
Cynomolgus = *Macaca fascicularis*
Gymnopyga = *Macaca maurus*
Hapale = *Callithrix*
Hemilago = *Galago (Galagoides)*

Inuus = *Macaca sylvana*
Kasi = *Presbytis*
Lagothrix hendeei = *L. flavicauda*
Lasiopyga = *Cercopithecus*
Leontocebus = *Leontideus and Saguinus*
Lichanotus = *Avahi*
Lyssodes = *Macaca*
Macaca irus = *Macaca fascicularis*
Macaca rhesus = *Macaca mulatta*
Macaca speciosa = *Macaca arctoides*
Maimon = *Papio*
Marikina = *Saguinus (Marikina)*
Mico = *Callithrix*
Midas = *Saguinus*
Mycetes = *Alouatta*
Mystax = *Saguinus*
Nomascus = *Hylobates concolor*

<i>Oedipomidas</i>	= <i>Saguinus</i> (<i>Oedipomidas</i>)	<i>Semnopithecus</i>	= <i>Presbytis</i>
<i>Otolemur</i>	= <i>Galago crassicaudatus</i>	<i>Silenus</i>	= <i>Macaca</i>
<i>Papio comatus</i>	= <i>Papio ursinus</i>	<i>Simia satyrus</i>	= <i>Pongo pygmaeus</i> or <i>Pan troglodytes</i>
<i>Papio doguera</i>	= <i>Papio anubis</i>		
<i>Pithecus</i>	= <i>Presbytis</i> , etc.	<i>Simia</i>	= <i>Papio. Pan. Macaca sylvana. Pongo</i>
<i>Presbytis femoralis</i>	= <i>Presbytis melalophos</i>	<i>Tamarin</i>	= <i>Saguinus</i>
<i>Presbytis maurus</i>	= <i>Presbytis cristatus</i>	<i>Tamarinus</i>	= <i>Saguinus</i>
<i>Presbytis pyrrhus</i>	= <i>Presbytis cristatus</i>	<i>Tana</i>	= <i>Tupaia</i> (<i>Lyonogale</i>)
<i>Presbytiscus</i>	= <i>Rhinopithecus avunculus</i>	<i>Tarsius carbonarius</i>	= <i>Tarsius syrichta</i>
<i>Prolemur</i>	= <i>Hapalemur simus</i>	<i>Tarsius philippinensis</i>	= <i>Tarsius syrichta</i>
<i>Rhesus</i>	= <i>Macaca</i>	<i>Trachypithecus</i>	= <i>Presbytis</i>
<i>Rhinostigma</i>	= <i>Cercopithecus hamlyni</i>	<i>Troglodytes</i>	= <i>Pan</i>
<i>Saguinus spixii</i>	= <i>Saguinus geoffroyi</i>	<i>Zati</i>	= <i>Macaca</i>

3. COMMON NAMES OF PRIMATES

The principal synonyms for lemurs, monkeys and apes are listed below. This list is not definitive but includes all the common English, German, Dutch and French names for primate species. Purely local or dialect names are not included unless they have become adopted by American or European usage.

COMMON NAME	GENERIC NAME	SPECIFIC NAME
Abyssinian guereza	<i>Colobus</i>	<i>C. guereza</i>
Agile Gibbon	<i>Hylobates</i>	<i>H. agilis</i>
Agile Mangabey	<i>Cercopithecus</i>	<i>C. galeritus agilis</i>
Allen's Galago	<i>Galago</i>	<i>G. alleni</i>
Allen's Monkey	<i>Cercopithecus</i>	<i>C. nigroviridis</i>
Ampongi	<i>Avahi</i>	<i>A. laniger</i>
Angwantibo	<i>Arctocebus</i>	<i>A. calabarensis</i>
Anubis baboon	<i>Papio</i>	<i>P. anubis</i>
Ashy Titi	<i>Callicebus</i>	<i>C. moloch donacophilus</i>
Assamese macaque	<i>Macaca</i>	<i>M. assamensis</i>
Atbarapavian	<i>Papio</i>	<i>P. anubis</i>
At��le araign��e	<i>Brachyteles</i>	<i>B. arachnoides</i>
Aye-Aye	<i>Daubentonia</i>	<i>D. madagascariensis</i>
Azara's Capuchin	<i>Cebus</i>	<i>C. apella cay</i>
Babakoto	<i>Indri</i>	<i>I. indri</i>
Baboons	<i>Papio</i>	
Babouin	<i>Papio</i>	
Bald Chimpanzee	<i>Pan</i>	<i>P. troglodytes</i>
Bald Leaf Monkey	<i>Presbytis</i>	<i>P. frontatus</i>
Bald Tamarins	<i>Saguinus</i>	
Bald Uakari	<i>Cacajao</i>	<i>C. calvus</i>

COMMON NAME	GENERIC NAME	SPECIFIC NAME
Widow Monkey	<i>Callicebus</i>	<i>C. torquatus</i>
Wied's Tamarin	<i>Leontideus</i>	<i>L. chrysomelas</i>
Wieselmaki	<i>Lepilemur</i>	<i>L. mustelinus</i>
Wolf's Monkey	<i>Cercopithecus</i>	<i>C. wolfi wolfi</i>
Wollaffe	<i>Lagothrix</i>	
Wollmaki	<i>Avahi</i>	<i>A. laniger</i>
Woolly Lemur	<i>Avahi</i>	<i>A. laniger</i>
Woolly Monkeys	<i>Lagothrix</i>	
Woolly Spider Monkey	<i>Brachyteles</i>	<i>B. arachnoides</i>
Yellow Baboon	<i>Papio</i>	<i>P. cynocephalus</i>
Yellow Monkey	<i>Cercopithecus</i>	<i>C. pygerythrus johnstoni</i>
Yellow-Nosed Monkey	<i>Cercopithecus</i>	<i>C. ascanius whitesidei</i>
Zweifarben Tamarin	<i>Saguinus</i>	<i>S. bicolor</i>
Zwergchimpanzee	<i>Pan</i>	<i>P. paniscus</i>
Zwergmeerkatze	<i>Cercopithecus</i>	<i>C. talapoin</i>
Zwergpavian	<i>Papio</i>	<i>P. anubis neumanni</i>
Zwergseidenäffchen	<i>Cebuella</i>	
Zwerg-"Siamang"	<i>Hylobates</i>	<i>H. klossii</i>
Zotteleaffe	<i>Pithecia</i>	<i>P. monachus</i>

4. TAXONOMIC NOTES

Alouatta

Following Hall and Kelson (1959), the specific name *Alouatta palliata* Gray, 1849, for the Central American or Mantled Howler, is rejected on the grounds that it is antedated by *A. villosa* Gray, 1845.

According to Hershkovitz (1964), *A. fusca* E. Geoffroy, 1812 is the correct name for the brown howler, *A. guariba* Humboldt, 1812 being a junior homonym of *A. guariba* E. Geoffroy, 1806.

Avahi

Following Schwarz (1931, *Proc. zool. Soc. Lond.*, p. 425, footnote), the prior *Lichanotus* Illiger, 1811 has been rejected as it is a synonym of *Indri* Geoffroy and Cuvier, 1795, containing the same two species.

Cacajao

In this genus Fiedler (1956) and Hill (1960) include four species, one of which, *Cacajao roosevelti* Allen, 1914, is considered to be a synonym of *Chiropotes albinasus* (Goodwin, G. G. *Bull. Am. Mus. nat. Hist.* 102: 262, 1953).

Callimico

The genus *Callimico*, with 36 teeth as in Cebidae, and claws on hands and feet as in Callitrichidae, has given rise to differences of opinion as to its systematic position. It is usually considered as the sole genus of subfamily Callimiconinae. Simpson (1945) placed Callimiconinae in the Cebidae, considering the dental characters to be more important taxonomically than the characters of the hands and feet; in this, he was followed by Cabrera (1957). Pocock (1925c) and Wood Jones (1929) were exponents of the opposite view. From recent anatomical studies, Hill (1957: Preface, p. viii) concludes that *Callimico* is a primitive tamarin, and therefore that Callimiconinae must be placed in the Callitrichidae, a view that is followed here.

Callithrix

Although Simpson (1945) includes *Cebuella* in the genus *Callithrix*, it is retained here as a separate genus, following Cabrera (1957). The Bare-eared Marmoset, placed in the genus *Mico* Lesson, 1840, by Hill (1957), is considered a species of *Callithrix*, *C. argentata*. See Comparative Taxonomy of the Callitrichinae below.

COMPARATIVE TAXONOMY OF THE CALLITRICHINAE (Generic Name)

	Simpson 1945	Herskovitz 1949a	Cabrera 1957	Hill 1957	Hill 1960	Herskovitz 1966a and b
Marmosets: ("short-tusked"; i.e. with elongated lower incisors and incisiform lower canines)						
Typical Marmosets	<i>Callithrix</i>		<i>Callithrix</i>	<i>Hapale</i>	<i>Hapale</i>	<i>Callithrix</i>
Bare-eared Marmosets	<i>Callithrix</i>		<i>Callithrix</i>	<i>Mico</i>	<i>Mico</i>	<i>Callithrix</i>
Pygmy Marmosets	<i>Callithrix</i>		<i>Cebuella</i>	<i>Cebuella</i>	<i>Cebuella</i>	—
Tamarins: ("long-tusked"; i.e. with normal lower canine-incisor relationship)						
Black-faced hairy-faced Tamarins	<i>Leontocebus</i>	<i>Marikina</i> (<i>Tamarin</i>)	<i>Leontocebus</i> (<i>Tamarin</i>)	<i>Tamarin</i>	<i>Tamarin</i>	<i>Saguinus</i>
White-moustached hairy- faced Tamarins	<i>Leontocebus</i>	<i>Marikina</i> (<i>Tamarin</i>)	<i>Leontocebus</i> (<i>Tamarin</i>)	<i>Tamarinus</i>	<i>Leontocebus</i>	<i>Saguinus</i>
Bare-faced Tamarins	<i>Leontocebus</i>	<i>Marikina</i> (<i>Marikina</i>)	<i>Leontocebus</i> (<i>Marikina</i>)	<i>Marikina</i>	<i>Marikina</i>	<i>Saguinus</i>
Crested Bare-faced Tamarins or Pinchés	<i>Leontocebus</i>	<i>Marikina</i> (<i>Oedipomidas</i>)	<i>Leontocebus</i> (<i>Oedipomidas</i>)	<i>Oedipomidas</i>	<i>Oedipomidas</i>	<i>Saguinus</i>
Golden Lion Tamarins	<i>Leontocebus</i>	<i>Leontocebus</i>	<i>Leontideus</i>	<i>Leontocebus</i>	<i>Leontideus</i>	

Cebuella

Although Simpson (1945) includes *Cebuella* in the genus *Callithrix*, it is retained here as a separate genus, following Cabrera (1957). See Comparative Taxonomy of the Callitrichinae, above.

Cercocebus

Schwarz (1928a) provides for four species of *Cercocebus* in two species-groups. Booth (1956b) shows *C. atys* to be a separate species with two races. Following Booth, we have included *C. atys* in Schwarz' *torquatus* group. For subspecies of the genus, we have followed Schwarz (*loc. cit.*). A useful discussion of the place of mangabeys in the systematics of Cercopithecinae is that of Tappen (1963).

Cercopithecus

Taxonomy of *Cercopithecus* is still largely a matter of dispute and is likely to remain so until the whole genus is reviewed from an ecological as well as a morphological viewpoint, particularly the *mitis*, *cephus* and *nictitans* groups.

We have followed Allen's (1939) revision of Schwarz' (1928b) classification for species groups, excepting for *C. talapoin*. Schwarz (*loc. cit.*) regarded all closely related groups that replace each other geographically as subspecies regardless of biological considerations; thus Schwarz' "species-groups" are in effect species containing a number of subspecies. The species-group concept is broadly equivalent to the taxon "superspecies" suggested by Rensch (1929), discussed at length by Mayr (1963) and used for *Cercopithecus* by Hill (1966b).

C. talapoin and *C. nigroviridis* we have placed in separate subgenera; this procedure follows that of Fiedler (1956) in the case of *C. nigroviridis*. Verheyen (1962) also has three subgenera including *Erythrocebus* and *Allenopithecus* but not including the talapoin monkey which is placed within the subgenus *Cercopithecus*. Rode (1938) would include *Miopithecus* as a separate genus; and Zuckerman (1933) accepts generic status for the talapoin on the important grounds of its sexual skin. Hill (1966b) places *Allenopithecus* and *Miopithecus* in separate genera.

We have followed Booth's (1955) revision of Mona monkeys in which five species, e.g. *C. mona*, *C. campbelli*, *C. wolffi*, *C. pogonias* and *C. denti* are included within the Mona group (also Hill, 1966b).

For species and subspecies we have followed Hill (1966b).

Colobus

Many modern authors place all African Colobinae in one genus (Allen, 1939, Rode, 1937, and Fiedler, 1956) following Schwarz, 1929. Schwarz (*loc. cit.*) placed all black and white *Colobus* in a single species, *polykomos*, with four sections, i.e. *polykomos*, *satanas*, *angolensis* and *abyssinicus*. Pocock (1936) did not accept Schwarz' view, preferring to regard Schwarz' "sections" as species. Booth (1954) also regards Schwarz' procedure as an oversimplification. Rode (1937) follows Schwarz except for *C. satanas* which he separates; Fiedler (1956) does likewise though he retains *satanas* in the *polykomos* species section. Allen (1939) in his Checklist of African Mammals includes all the black and white group under *C. polykomos*. Verheyen (1962), on the basis of skull morphology, recognizes two good species: *C. polykomos* and *C. abyssinicus* (= *guereza*), a procedure that is followed here. Verheyen (*loc. cit.*) treats *C. satanas* as a race of *C. polykomos*.

Pocock (1936) separates *Procolobus* Rochebrune 1887 from *Colobus*, with *verus* Van Beneden, 1838 as the type; within this genus, Pocock includes the red colobus group. Hill (1952), after studying the external and visceral anatomy of *Procolobus*, reserves this name for the olive

species, *verus*. Hill points out that, if this position is accepted, the red Colobus must be separated at generic level; he recommends resuscitation of *Piliocolobus* Rochebrune 1887 for the *badins* group, a recommendation followed by Booth (1954).

Verheyen (1962), on craniological and craniometric evidence, gives *Procolobus* and *Piliocolobus* subgeneric status within the genus *Colobus*, a procedure that is followed here.

The name, *Colobus abyssinicus* Oken, 1816, for the Abyssinian Colobus, is not available (International Commission on Zoological Nomenclature, Opinion 417, 1956). The next available name, *Colobus guereza* Rüppell, 1835, is therefore employed.

Cynopithecus

At present only a tentative arrangement is possible with regard to the Celebes monkeys. Büttikofer (1917), although placing all the Celebes monkeys in the genus *Cynopithecus*, divides them into two distinct groups: "Macaques" (5 species), and "Crested Macaques" (3 species). In his "Crested Macaques" group, he includes *C. niger* Desmarest, 1822, *C. nigrescens* Temminck, 1849 and *C. becki* Matschie, 1901. Laurie and Hill (1954) consider these to be synonymous; following their checklist, *Cynopithecus* is here retained as a separate genus with one species *C. niger*.

Galago

Schwarz (1931a) recognized two genera, *Galago* and *Euoticus*, within the Galaginae. Hill (1953) prefers to remove *G. demidovii* from *Galago* and place it in a separate genus *Galagoides* A. Smith, 1833, principally on account of its distinctive placentation (Gérard, 1929, 1931 and 1932; but see J. P. Hill, 1965).

Fiedler (1956) has relegated both *Euoticus* and *Galagoides* to subgenera of *Galago*, a procedure followed here on the grounds, as far as *Euoticus* is concerned, of Hayman's (1937) observation that *G. senegalensis inustus* Schwarz, 1930 also presents the unguis specializations of *Euoticus* and should be placed in this genus. *Inustus*, it would appear, is the link which indicates the true taxonomic affinities of *Galago* and *Euoticus*. It does not appear to us that *Galagoides* is sufficiently distinct from *Galago* or *Euoticus* to be separated generically. For subspecies, we have followed Allen (1939) and Hill (1953).

Gorilla

The accepted classification of gorillas (Coolidge, 1929) divides the species into two subspecies: *G. g. gorilla* (western or lowland gorillas) and *G. g. beringei* (eastern or mountain). Except that some authors prefer to regard these two as full species, the Coolidge revision is generally employed today. However, not only did Haddow and Ross (1951) point out irregularities in Coolidge's methods, but recently the realization has been growing that not all eastern gorillas live on mountains.

A recent revision (Groves, 1966) recognizes the eastern lowland gorillas as forming a third subspecies (*G. g. manyema* Rothschild, 1908) equidistant from the other two; distinguishing characters are to be found in both skull and postcranial skeleton. The gorillas of the Mitumba mountains of the eastern Congo are somewhat intermediate between the subspecies *manyema* and *G. g. beringei* of the Virunga Volcanoes—in skull morphology as well as in altitude—but are morphologically nearer to the former, probably because of genetic continuity.

Hylobates

Many authors, including Miller (1933), Ellerman and Morrison-Scott (1951) and Simonetta (1957), place all the Gibbons and the Siamang in one genus with four subgenera. Following Schultz (1930 and 1933b), *Symphalangus* is here given generic status, but the subgenera *Brachitanytes* (Schultz, 1932) and *Nomascus* (Miller, 1933) are not employed.

Although Schultz (1933b) gives *Hylobates pileatus* and *Hylobates leucogenys* specific status, they are here given only subspecific rank, following Ellerman and Morrison-Scott (1951), Delacour (1951), and Simonetta (1957). The latter author makes the Sunda Island Gibbon (*H. moloch*) conspecific with *H. lar*, following Sody (1949).

Lagothrix

On his travels in South America, Humboldt saw dark-brown furry skins used as saddle-cloths by the Peruvians for their mules. On the basis of these skins he described (1812) a new species of Howler monkey which he named *Simia flavicauda*. Thomas (1927a) described a newly discovered monkey from Peru as *Lagothrix (Oreonax) hendeei*. It was very similar to *Simia flavicauda* Humboldt, particularly in the yellow-striped prehensile tail, but Thomas in a further paper (1927b) maintained that the two were taxonomically distinct. Cabrera (1957) considered *Simia flavicauda* Humboldt to be indeterminable. Fooden's arguments in favour of *L. hendeei* Thomas and *S. flavicauda* Humboldt being identical are set forth on pp. 242 and 243 of his paper "A revision of the woolly monkeys (Genus *Lagothrix*)" (*J. Mammal.* **44**: 213-247, 1963).

Lemur

Following Schwarz (1936) and Petter (1962c), *Lemur fulvus* is accepted as conspecific with *L. macaco* in view of their many similarities of structure and behaviour and, more significantly, of the existence of intermediate forms (*L. fulvus flavifrons* and *L. fulvus sanfordi*) as discussed by Petter (1965). *L. macaco* Linnaeus, 1766 has priority over *L. fulvus* E. Geoffroy, 1812.

Petter (1962c), following Gray (1863), proposes to separate *L. variegatus* generically from *Lemur* and place it in a monotypic genus *Varecia*. It does not appear to us that there is sufficient evidence at this time to justify such a step—although we recognize that it may well become necessary.

Lepilemur

The genus *Lepilemur* has recently been reviewed by Petter (1960) who regards it as consisting of a single species, *Lepilemur mustelinus* I. Geoffroy, 1851, with five subspecies.

He further suggests (1965) that from the point of view of ecology and ethology this genus differs profoundly from the remaining members of the Lemurinae. Morphologically, as Mivart (1873) was the first to observe, many characters of the vertebral column, thorax and hand, link this genus with the Indriidae, with which family *Lepilemur* shares its locomotor characteristics. The similarity of locomotor behaviour is reflected in similarity of limb and hand proportions. Davies and Hill (1954a) comment on the differences in gastric morphology of *Lepilemur* from that of other Lemurinae, indicating that, in certain features,

it resembles that of *Propithecus* and other primate leaf-eaters; at the same time Davies and Hill point out the many similarities of the alimentary system with other Lemurinae. There seems little doubt in view of the wide dissimilarity in the dentition (*inter alia*) that this affinity is a matter of parallelism arising in two separate groups having a common ancestral stock in which, as it now seems possible (Napier and Walker—in press), vertical clinging and leaping was the typical mode of locomotion. The authors, in support of Petter's recommendation, suggest that *Lepilemur* be placed in a separate subfamily of Lemuridae, the Lepilemurinae.

Macaca

Pending the comprehensive revision of the genus by Fooden, the checklists of Allen (1939), Chasen (1940), Ellerman and Morrison-Scott (1951) and Laurie and Hill (1954) are combined here; an additional subspecies of *M. maurus* (*ochreata* Ogilby, 1840) is included in the systematic list (Hooijer, 1950). The Philippines macaques recognized by Lawrence (1939): *M. mindora* Hollister, 1913, and by Sanborn (1952): *M. philippinensis philippinensis* Geoffroy, 1843 and *M. philippinensis mindanensis* Mearns, 1905, are here considered as subspecies of *M. fascicularis*.

Macaca fascicularis Raffles, 1821 replaces *M. irus* F. Cuvier, 1818 as the earliest name properly proposed for the crab-eating macaque (Miller, 1942, Fooden, 1964a). The name, *Macaca speciosa* I. Geoffroy, 1826, used in the text for the stump-tailed macaque, must in future be replaced by *Macaca arctoides* I. Geoffroy, 1831 (see Fooden, 1967).

In spite of Fooden's proposition (1964a) that the crab-eating macaque, *M. fascicularis*, and the rhesus macaque, *M. mulatta*, should be considered conspecific, they are here retained as separate species.

Mandrillus

M. poensis Zukowsky, 1922, is a subspecies of *M. leucophaeus* from Fernando Póo, distinguished by its small size. Tappen (1960) proposed that it should be granted specific rank.

M. insularis Zukowsky, 1925 (a Mandrill), was also said to be from Fernando Póo, but this is probably a mistaken locality.

Nycticebus

A new species, *N. intermedius*, based on an adult ♀ from Hoa Binh, North Vietnam, has been described by Tien (1960); it is intermediate in size between *N. coucang* and *N. pygmaeus* (Head and body length: 230 mm 1♀).

Pan

Validation of generic name: The name *Pan* was first published by Oken in "*Lehrbuch der Naturgeschichte*" Vol. 3, 1816, a work rejected by the International Commission on Zoological Nomenclature on nomenclatorial grounds in Opinion 417, 1956. The next available name is *Chimpansee* Voigt, 1831 (HersHKovitz, 1949b). Ruling 3 of Opinion 417 invited zoologists to submit applications for the validation, under the plenary powers of the Commission, of any of Oken's names, if, in their opinion, rejection would lead to instability or confusion in nomenclature. Application for the validation of *Pan* was made in 1950 and revised in 1965. Consequently the generic name for the chimpanzee is at present *sub judice* and current usage (*Pan* Oken, 1816) is therefore continued here. (Article 80, *International Code of Zoological Nomenclature*, 1964.)

Races of Chimpanzee: A fourth race of *P. troglodytes*, *P. t. calvus* du Chaillu, 1860, is sometimes recognized. The common names for *P. t. calvus* are the Choga, the Black-faced Chimpanzee and the Kooloo-kamba. This form is here regarded as synonymous with *P. t. troglodytes*.

The distinguishing features of *P. t. calvus* are a black face, black hands and feet, and a gorilla-like external nose resembling a "squashed tomato" (L. G. Smith—private communication). Its distribution is said to be from the Cameroons south to Gabon. Rode (1936) points out that with age the pigmentation of the face of *P. t. troglodytes* "... devient plus foncée et finalement noire". He also observes that among adult chimpanzees in the wild pigmentation of the face is more marked than it is in captivity in temperate climatic zones, which may explain why Kooloo-kambas appear to be more common in Africa than in European Zoos!

The Bonobo or pygmy chimpanzee: the Bonobo was first described as a subspecies of *P. troglodytes* by Schwarz (1929). Its taxonomic position was discussed by Coolidge (1933b) and by Schouteden (1931). In 1954, Tratz and Heck placed it in a separate genus, *Bonobo*. Here, the authors have followed Allen (1939) in giving the Bonobo full species rank.

Papio

Müller's description of *Papio* (1776) referred to a mandrill (Hopwood, 1947). Unless therefore mandrills are included in the genus (see Fiedler, 1956) the taxon is invalid for typical baboons and *Chaeropithecus* Gervais, 1839 becomes the valid name; this nomenclature is followed by Ellerman, Morrison-Scott and Hayman (1953). *Papio* Erxleben, 1777, though strictly invalid, is here retained in the interests of stability. In the light of the most recent revision (Jolly, 1964), *P. hamadryas* is placed in the genus *Papio* but in a separate species group. We regard, as the correct name for the olive baboon, *Papio anubis* Lesson, 1827 [= *P. doguera*] (Hill, 1959; Hershkovitz, 1960), and for the Chacma baboon, *Papio ursinus* Kerr, 1792 [= *P. comatus*].

Presbytis

Following Ellerman and Morrison-Scott, 1951, and Chasen, 1940, the Asiatic Colobinae are placed in five genera: *Rhinopithecus*, *Pygathrix*, *Nasalis*, *Simias* and *Presbytis*: the latter is divided into four species groups which have sometimes been given generic status (see Hill, 1939a; Pocock, 1939; Washburn, 1944, and Hooijer, 1962) as follows:

<i>Presbytis aygula</i> group [= <i>Presbytis</i> Eschscholtz, 1821]	4 species
<i>Presbytis entellus</i> group [= <i>Semnopithecus</i> Desmarest, 1822]	1 species
<i>Presbytis senex</i> group [= <i>Kasi</i> Reichenbach, 1862]	2 species
<i>Presbytis cristatus</i> group [= <i>Trachypithecus</i> Reichenbach, 1862]	7 species.

A possible eighth species of the *P. cristatus* group, *P. leucocephalus*, has been described by Pang-Chieh (1957); limited range in Fusui country (Funan, S. Kwangsi). See also Jarvis (1966).

Saguinus

Leontocebus Wagner, 1840, is rejected as the valid name for the tamarins (other than the Golden Lion Tamarin, *Leontideus rosalia* Linnaeus, 1766) because it is antedated by *Saguinus* Hoffmannsegg, 1807. Moreover, the retention of *Leontocebus* for this group may cause

confusion; since 1912, when Miller (*U.S. nat. Mus. Bull.* 79: 380) selected as the type species *Midas leoninus* Geoffroy, 1812 (= *Simia leonina* Humboldt, 1812 (*Rec. Obs. Zool.*, p. 14, plate 5), *Leontocebus* has been considered to be allied to or identical with *Leontideus rosalia*, the Golden Lion Tamarin. Humboldt's figure, Plate 5, gives the impression of a golden-maned tamarin. However, in 1956 Cabrera drew attention to the discrepancies between the drawing (by an artist who never saw the animal) and Humboldt's description; he showed that Humboldt's animal was a white-moustached tamarin and *not* a maned tamarin. For the maned tamarins of the *rosalia* type, Cabrera proposed a new genus name *Leontideus* (Type species: *Simia rosalia* Linnaeus, 1766). Thus, the name *Leontocebus*, for many years associated with a maned tamarin, now means every other type of tamarin but that one, i.e. the hairy-faced tamarins (with or without white moustache) = *Saguinus* (*Saguinus*); the bare-faced tamarins = *Saguinus* (*Marikina*); and the crested bare-faced tamarins or Pinchés = *Saguinus* (*Oedipomidas*).

The above arrangement of the tamarins is that of Hershkovitz (1949a) and Cabrera (1957); Hershkovitz (1966a) uses species groups, rather than subgenera, to indicate the groupings of the different forms of the genus. See Comparative Taxonomy of the Callitrichinae, p. 371.

Saimiri

Cabrera (1957) considered that, pending a conscientious revision of the genus, the numerous species which have been described must be reduced to two, *S. sciureus* (from South America) and *S. oerstedii* (from Central America), and that even the latter is possibly only a subspecies of the former. Cabrera's arrangement is followed here.

Hill (1960), following Cruz Lima (1945) recognizes four South American species; for descriptions and localities, see Hill (1960, 1965).

As *Saimiri* is in extensive use as a laboratory animal, basic work on the taxonomy of the genus is overdue (Hershkovitz, 1965).

Symphalangus

A. H. Schultz, in his paper "Observations on the growth, classification and evolutionary specialization of Gibbons and Siamangs" (*Hum. Biol.* 5: 212-255, 385-428, 1933), places *Symphalangus*, on account of its many distinctive morphological characters, in a separate genus, an arrangement which is followed here.

Tupaia

For the classification of the Tupaiinae the authors have followed Lyon (1913) and Simpson (1945) in retaining four genera (*Tupaia*, *Anathana*, *Dendrogale* and *Urogale*) within the subfamily. They feel, however, that in the light of modern taxonomic trends a fresh look at the Tupaiinae will lead to a reduction in the number of genera. Fiedler (1956) already includes *Anathana* in the genus *Tupaia*.

Lyonogale Conisbee, 1953 [= *Tana* Lyon, 1913] has been retained as a subgenus of *Tupaia*, following Medway, 1965. *Lyonogale* was considered by Chasen and Kloss (1931) and Davis (1962) to be inseparable from *Tupaia*, a view accepted by Fiedler (1956).

The subgeneric name *Lyonogale* is substituted for the preoccupied *Tana* Lyon, 1913 (see Conisbee, 1953).

Habitats of Primates

1. GEOGRAPHICAL RANGE

With very few exceptions, the vast majority of living primates are restricted to the tropics. In this region, their main habitats are the forests and the savannahs between the latitudes 25° N and 30° S. As a rule, primates do not extend into temperate zones, in fact the macaques (and possibly *Rhinopithecus*) are the only primates to have done so (Fig. 4). In China, macaques (*M. mulatta*) are found near Pekin although it may well be that they were introduced there. In Japan, the Japanese macaque (*M. fuscata*) reaches as far north as 41° on the island of Honshu. Limiting factors to the northerly migration of primates in Asia are concerned partly with temperatures but particularly with food-availability (Jolly, 1964). The higher the latitude, the more restricted becomes the growing season and the shorter the daylight period in winter. The combination of these two factors would make it extremely difficult for monkeys to find sufficient food during the daylight hours. African primates seem to be able to adapt well to cold conditions so that low temperatures alone would not be expected to limit their range. New World monkeys on the other hand appear to be extremely sensitive to temperatures much below 70° F.

The main blocks of primate distribution are (1) African (including Madagascan), (2) South-east Asian and (3) South American. Whereas S. American stocks have been independent since the Eocene, the African and Asian stocks are closely related and share members of four sub-families, i.e. Colobinae, Cercopithecinae, Lorissinae and Ponginae. The only common genus to the African and South-east Asian blocks is *Macaca*.

Apart from the main primate blocks there are a number of islands on which primates are found today; here they live as natural populations, descendants of forms introduced, in the first place, by man. In the West Indies, on the islands of St. Kitts and Grenada, are populations of *Cercopithecus sabaens* and *Cercopithecus mona* respectively; *Macaca fascicularis* [= *irus*] are to be found on the island of Mauritius. The only monkeys resident on the continent of Europe are the Barbary "apes" of Gibraltar (*M. sylvana*) introduced sometime prior to 1704 when the British took over. In a somewhat different category, are the research islands such as Barro Colorado in the Panama Canal and Cayo Santiago in the Caribbean. In the former live a number of New World genera including howlers, spider monkeys and capuchins; on Cayo Santiago there is a thriving study colony of *Macaca mulatta* introduced some 25 years ago.

2. ECOLOGY IN AFRICA

In Africa, bordering the savannah belt to the north and south, and constituting formidable ecological barriers to primate migration, are belts of arid grasslands, desert and scrub. Some of the savannah-living African primates, such as the baboons, range beyond the limits of the savannah belt into sub-desert regions.

The vegetational zonation in Central Africa is seen in Fig. 6, which represents a sample strip of West Central Africa some 1300 miles in length, extending from the Congo (Brazzaville) in the south on the Equator, northwards through the Ubangi-Shari, Chad and ending south

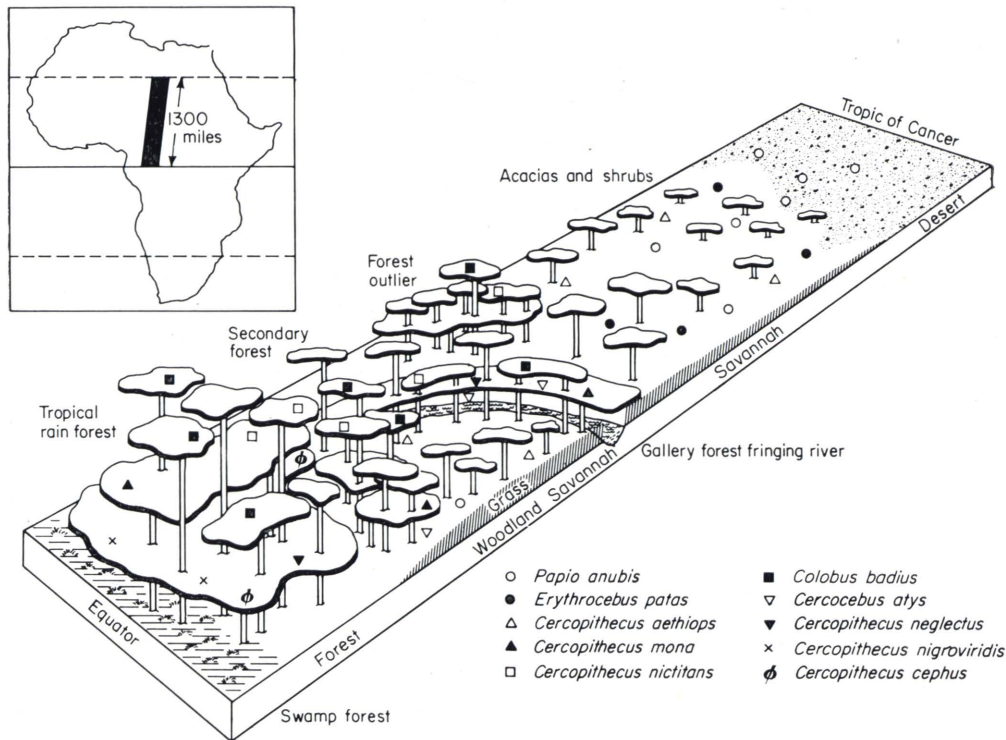


FIG. 6. Vegetational zones in sample strip 1300 miles in length from Congo to Tibesti plateau showing resident primates

of Tibesti. Altitudinal differences are not considered in this strip which, in fact, represents a plateau varying between 1000 and 2500 feet above sea level. The main vegetational zones lie in an east-west direction roughly parallel to the Equator, the width of each zone being determined by local climatic factors of rainfall and temperature. Generally speaking rainfall decreases from south to north. In the equatorial region the temperature is high all the year round and the rainfall is continuous showing two maxima in May-June and September-October. These conditions change at about 5° N to a climate where temperatures are even higher at the maximal point of the annual range which occurs in March; about 40 inches of rain fall in the summer, but the winters are dry. At 15° N grassland begins to give way to shrub and finally to desert where temperatures show marked seasonal fluctuations and rainfall is practically nil. In vegetational terms the main succession is: (1) tropical rain forest: (2) savannah: (3) steppe: (4) desert. (Table I.)

TYPE 1. TROPICAL RAIN FOREST BIOME

The chief characteristic is a dense evergreen closed canopy with abundance of thick-stemmed lianes and herbaceous epiphytes. Many of the trees bear buttress roots. There is an absence of grasses on the forest floor which supports ill-defined herb and shrub strata. The forest canopy is itself stratified into three more or less well-defined storeys, the highest storey extending up to 150 feet or more (Richards, 1957). There are a number of sub-types (Table I) of tropical rain forest including mangrove swamp, swamp forest, secondary forest and montane forest.

Primate Fauna

There are two major habitats within a tropical rain forest and a number of minor ones. The major habitats are the forest floor and the canopy (here used to indicate all the crowns of trees above the shrub layer). The principal primate inhabitants of the floor in West Central Africa are *Mandrillus*, *Pan* and *Gorilla gorilla*; in the canopy a variety of *Cercopithecus*, *Colobus* and *Cercocebus* are found. The prosimians are represented by *Galago*, *G. (Euoticus)*, *Perodicticus* and *Arctocebus*.

TYPE 2. SAVANNAH BIOME

Salient features of savannah are a mixture of grassland and trees. The two main sub-types are Woodland Savannah and Open Savannah. Tall grasses, which show a seasonal cycle terminated by burning, are the dominant vegetation of the Woodland Savannah. Open savannah has widely spaced flat-topped trees, 20–30 ft high, acacias (fever trees, umbrella trees) and boababs being frequent varieties. Common sub-types in savannah country are *gallery forests* bordering streams and *forest outliers*; both vegetational types are closely related to rain forest morphologically and occur where soil conditions are favourable, e.g. along banks of rivers or streams and in moist, well-drained valleys.

Primate Fauna

In the savannah of the Central African Republic the more terrestrial of the guenons are found, particularly the *Cercopithecus aethiops* group. Among the fully terrestrial forms *Papio* and *Erythrocebus* abound. In gallery forests and rain forest outliers *Colobus*, *Cercopithecus* and *Cercocebus* (especially *C. galeritus* and *C. atys*) are found; also *Galago*.

TYPE 3. STEPPE BIOME

This zone which bears a variety of regional synonyms (e.g. Thornland in French Equatorial Africa) forms a transition between savannah and desert. Low, widely-spaced acacias and other spiny trees are characteristic of this belt, where they form sporadic closed canopy thickets. Grass is in tussocks and rather sparse. The zone gradually deteriorates north of Lake Chad into sub-desert.

Primate Fauna

Only the thoroughly terrestrial genera, such as *Papio*, *Erythrocebus* and (more rarely) the grivets *C. aethiops*, inhabit the zone.

TYPE 4. DESERT BIOME

In the sub-Saharan zone of Chad the only vegetation consists of sparse dwarf shrubs whose life cycle occupies only a few weeks following the short, irregular rainy season. Further north there is barren desert with a rocky sub-stratum and a sandy soil; an occasional wadi relieves the monotony which, by virtue of subterranean water, can support sparse, perennial shrubs.

TABLE I

A Summary of the Vegetational Zones and Related Primate Fauna of Sub-Saharan Africa

	<i>Vegetation zone</i>	<i>Sub-type</i>	<i>Vegetation and climate</i>	<i>Primate genera</i>
<i>Type</i> <i>I</i>	Tropical rain forest Alternative terms: Moist forest Lowland rain forest Tropical high forest Forêt dense		3 strata constituting an open and closed canopy with emergents Temp.—steady with narrow range Rainfall—high Rel. humidity—high	<i>Cercopithecus</i> <i>Colobus</i> <i>Pan</i> <i>Gorilla</i> <i>Cercocebus</i> <i>Mandrillus</i> <i>Perodicticus</i> <i>Galago</i> <i>Arctocebus</i>
		Mangrove	Specialized mangroves lining estuaries and creeks to tidal limits	
		Secondary forest	Tropical rain forest that has been cultivated and subsequently abandoned	
		Swamp forest	Similar but more open and irregular in structure	
		Montane rain forest Alternative terms: Highland forest Cloud forest	3000 ft up to 8000 ft (depending on climatic conditions). Varies from evergreen forest to woodland with tree fern and bamboo thickets. Lianes	<i>Pan</i> <i>Gorilla</i> <i>Cercopithecus</i> <i>Colobus</i> <i>Papio</i>
		Bamboo forest	7000 ft–10,000 ft. Stands of bamboo from 20–35 ft. Ground cover sparse	
<i>Type</i> <i>II</i>	Savannah Alternative terms: Sour veldt (S.Af.) High grass (E.Af.)	Woodland	Trees 20 ft–50 ft high especially <i>Isobertlinia</i> Grass 6 ft–15 ft high	<i>Cercopithecus</i> (esp. <i>C. aethiops</i>) <i>Erythrocebus</i> <i>Colobus</i> <i>Papio</i> <i>Cercocebus</i> <i>Galago</i>
		Open savannah	Trees widely spaced Grass 6 ft–15 ft high	
		Forest outliers Alternative terms: Bowl forest Kurmi Copses	Islands of tropical rain forest. Occurs in hollows and ravines where edaphic conditions are favourable	
		Gallery forest Alternative terms: Riverine forest Fringing forest	Tropical rain forest on river banks	
<i>Type</i> <i>III</i>	Steppe Alternative terms: Thornland Sweet veldt (S.Af.) Short grass (E.Af.) Desert grass Orchard steppe	Wooded steppe	Open and closed woodlands or thickets. <i>Acacia</i> and <i>Commiphora</i> Short grasses	<i>Cercopithecus</i> (esp. <i>C. aethiops</i>) <i>Erythrocebus</i> <i>Papio</i>

Primate Fauna

Papio may range occasionally into this region.

While this account refers directly to the sample strip inset in Fig. 6, the succession is typical of many regions in Africa, north and south of the Equator. Table I includes the primate fauna inhabiting the strip, but also lists forms found in similar vegetational zones elsewhere in Africa, including montane and bamboo forest which does not appear on the strip.

3. MINOR HABITATS OF PRIMATES AND FOREST STRATIFICATION

It has become apparent in recent years that in order to assess the taxonomic inter-relationships of monkey populations, a vertical dimension must be added to the more familiar two-dimensional distribution or "range" maps. The forest canopy consists of several horizontal strata that provide a number of different ecological niches for tree-living fauna. This principle of stratification (a concept which recalls Humboldt's description of the Amazonian canopy as "a forest above a forest") has been known among botanists and foresters for some time, and

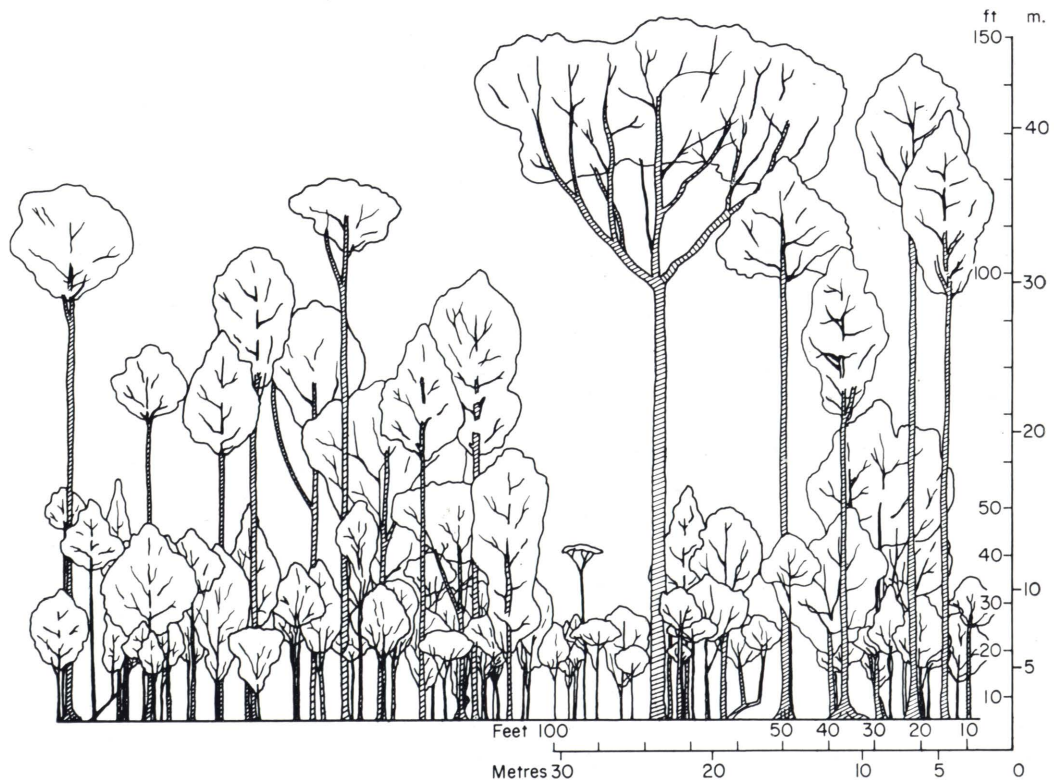


FIG. 7. Profile diagram of primary rain forest (Shasha Forest Reserve, Nigeria), showing stratification of canopy. Strip is 200 ft (6 m) long and 25 ft (7.6 m) wide. (From Richards, 1957, "Tropical Rain Forest", Cambridge University Press).

the existence of discrete storeys in tropical rain forest has been, and still is, a matter of considerable dispute. The situation has been largely resolved in certain areas by the technique of constructing profile diagrams of narrow sample strips of specially cleared forest (Fig. 7). Studies of stratification have been carried out in Nigeria, on the Ivory Coast, in Gabon, in Uganda, in South America and in the East Indies; although the edaphic conditions and the botanical nature of the tree and plant communities vary greatly from place to place, the principle of stratification appears to hold true.

Three strata are recognized. From below upwards, they consist of (1) understorey, 25–50 ft high; (2) middle storey, 50–120 ft high; (3) upper storey, 120–150 ft high.

The understorey consists of trees whose crowns, varying about a mean, form a completely *closed canopy*, the whole stratum being closely bound by woody creepers into a solid mass of foliage. The middle storey is an irregular layer of trees which occasionally form a closed canopy but whose crowns are usually in lateral contact. The upper storey consists of trees with broad umbrella-like crowns that form a discontinuous layer. In addition, giant trees (emergents) that reach as high as 200 ft are occasionally found. The lowest branches of one layer usually make contact with the highest branches of the layer below, so that the whole canopy constitutes a vertical continuum.

The principle of stratification of the tropical rain forest has opened a new field of study for primatologists that should lead to clarification of many taxonomic problems. In addition, this concept promises rich rewards for the study of locomotor behaviour and phylogeny.

TABLE II

Vertical Range of Monkeys in Forest of S.W. Ghana (Booth, A. H., 1956)

	Sleeping			Travelling				Feeding				Food	
	Upper	Middle	Lower	Upper	Middle	Lower	Ground	Upper	Middle	Lower	Ground	Fruit	Leaves
<i>Colobus badius</i>	+	-	-	++	+	-	-	++	+	(+)	-	-	+
<i>Colobus polykomos</i>	+	+	-	+	+	-	-	(+)	+	+	-	-	+
<i>Colobus verus</i>	-	+	+	-	+	+	-	-	(+)	+	-	-	+
<i>Cercopithecus diana</i>	+	+	-	+	+	-	-	+	+	(+)	-	+	-
<i>Cercopithecus campbelli</i>	-	+	(+)	(+)	+	+	(+)	-	+	+	-	+	-
<i>Cercopithecus petaurista</i>	-	+	+	-	+	++	(+)	-	(+)	++	-	+	+
<i>Cercocebus atys</i>	-	+	+	-	+	+	++	-	-	-	+	+	-

The principal implications of stratification *vis-à-vis* locomotor adaptations of primates are as follows:

- (1) The presence or absence of gaps between crowns of adjacent trees in relation to leaping and brachiating activities during travel.
- (2) The pattern of distribution and density of primate food items such as leaves, fruit and flowers, within the crowns of feeding-trees, in relation to the climbing behaviour and prehensile adaptations of the limbs of arboreally living primates.

With these implications in mind it is desirable that an attempt should be made to express stratification in terms that are more meaningful for primate biology than the A, B, C strata (or their synonyms) of botanical usage. It is suggested that for this purpose it is probably sufficient to divide the canopy simply into "open" and "closed" layers. The upper storey is invariably a discontinuous stratum whose component trees have umbrella-shaped crowns

(wider than deep) arising from a candelabra arrangement of distal branches (Richards, 1957). The maximum density of fruit and leaves thus tends to be sited peripherally; in order to reach and feed on the leaves, the animal is forced to move far out from the trunk into a milieu that is largely composed of small flexible branches; in such a setting the suspensory activities of the hands, feet and the balancing or suspensory activities of the tail (particularly in some New World monkeys) are called into play. The lower or under-storey invariably forms a continuous stratum with smaller crowns that are deeper than they are wide; at this level the leaves are more homogeneously distributed throughout the crown and feeding can be carried out largely in a dense milieu of rigid branches interlaced with lianes. This setting places, proportionately, a less intense demand on prehensility of extremities.

From the point of view of primate locomotion it would appear that animals that under experimental conditions select a small branch setting show a larger brachiation or arm-swinging component in their locomotor behaviour (Avis, 1962). Field observation, in addition, indicates that the black and white colobus monkeys (*Colobus polykomos* and *C. guereza*) which tend to be open canopy dwellers (Booth, 1957) cross wide gaps by leaping and swinging by the arms; this mode of locomotion of these animals has been termed semibrachiation (Napier, 1963). There is, thus, some evidence that the essential characteristics of the forest canopy for primate ecology are, firstly, a matter of *contiguity* of crowns; and secondly, of crown *shape* and *leaf density*; it would seem likely that both these factors may be correlated with stratification.

The trees of the middle storey of the canopy are characteristically in lateral contact (Richards, 1957) although there are frequently gaps between the crowns. The crowns themselves may be of either the upper or lower storey ("A" or "C" stratum) type. Therefore, whether the middle storey is to be grouped with the upper or lower storey for the purpose of the present classification, is somewhat equivocal. From the relatively few observations on stratification of living primate population, it would appear on the whole that there are more primate species which are common to both middle and lower storeys than there are species common to middle and upper storeys. (Booth, 1955, 1956, 1957; Haddow, 1952, Sanderson, 1940). In view of this it would seem more appropriate to place the middle storey with the lower storey in the following classification:

TABLE III

Open canopy	Crowns discontinuous	Broad, umbrella shaped crowns, with predominantly peripheral foliage	Upper storey
Closed canopy	Crowns in lateral contact or overlapping	Small narrow crowns with more homogeneously distributed foliage	Lower storey Middle storey

It is unnecessary to emphasize the provisional nature of this classification and the hypotheses on which it is based, but it may provide a useful starting point for further study of the ecology of arboreal primates. Many factors of primate behaviour and morphology, other than those mentioned, would have to be considered, particularly body size in relation to branch size and dietary preferences in relation to the preferred stratum.

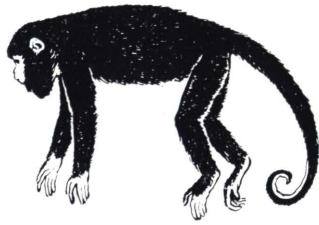
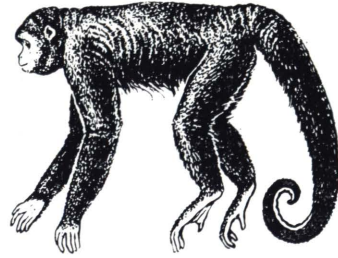
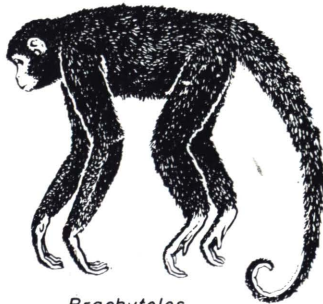
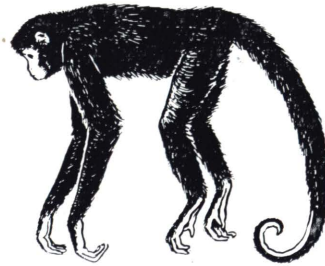
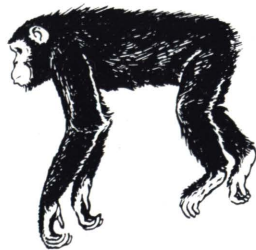
*Alouatta**Lagothrix**Brachyteles**Ateles**Hylobates**Pongo**Pan**Gorilla*

FIG. 8. Profile views of four New World monkeys (Semibrachiators) and four Anthropoid apes (Brachiators) reduced to common trunk length. By courtesy of G. E. Erikson, from "Brachiation in New World Monkeys and Anthropoid Apes" *Symp. Zool. Soc. Lond.* No. 10: 135-164.

Vital Statistics of Primates

I. GESTATION PERIODS OF PRIMATES

<i>Alouatta</i>	Not known	<i>Indri</i>	Not known
<i>Anathana</i>	Not known	<i>Lagothrix</i>	225 days approx.
<i>Aotus</i>	Not known	<i>Lemur</i>	120-135 days
<i>Arctocebus</i>	131 days*	<i>Leontideus</i>	Not known
<i>Ateles</i>	139 days approx.	<i>Lepilemur</i>	120-150 days
<i>Avahi</i>	Not known	<i>Loris</i>	160-174 days*
<i>Brachyteles</i>	Not known	<i>Macaca</i>	146-186 days
<i>Cacajao</i>	Not known	<i>Mandrillus</i>	245 days approx.
<i>Callicebus</i>	Not known	<i>Microcebus</i>	59-62 days
<i>Callimico</i>	Not known	<i>Nasalis</i>	166 days approx.
<i>Callithrix</i>	140 days	<i>Nycticebus</i>	193 days*
<i>Cebuella</i>	Not known	<i>Pan</i>	225 days
<i>Cebus</i>	180 days approx.	<i>Papio</i>	154-183 days
<i>Cercopithecus</i>	Not known	<i>Perodicticus</i>	Not known
(<i>Cercopithecus</i>)	180-213 days approx.	<i>Phaner</i>	Not known
<i>Cercopithecus</i>		<i>Pithecia</i>	Not known
(<i>Miopithecus</i>)	196 days*	<i>Pongo</i>	275 days
<i>Cheirogaleus</i>	70 days	<i>Presbytis</i>	168 days approx.
<i>Chiropotes</i>	Not known	<i>Propithecus</i>	150 days approx.
<i>Colobus</i>	Not known	<i>Ptilocercus</i>	Not known
<i>Cynopithecus</i>	155-175 days	<i>Pygathrix</i>	Not known
<i>Dendrogale</i>	Not known	<i>Rhinopithecus</i>	Not known
<i>Daubentonia</i>	Not known	<i>Saguinus</i>	140 days approx.
<i>Erythrocebus</i>	170 days (estimated)	<i>Saimiri</i>	168-182 days
<i>Galago</i>		<i>Simias</i>	Not known
<i>crassicaudatus</i>	130-135* days	<i>Symphalangus</i>	230-235 days
<i>Galago senegalensis</i>	144-146 days	<i>Tarsius</i>	180 days approx.
<i>Gorilla</i>	251-289 days	<i>Theropithecus</i>	Not known
<i>Hapalemur</i>	Not known	<i>Tupaia</i>	41-50 days
<i>Hylobates</i>	210 days approx.	<i>Urogale</i>	54-56 days approx.

* Based on one or two observations.

2. CHROMOSOME DIPLOID NUMBERS OF THE PRIMATES

[illegible]

	20 +	30 +	40	42	44	46	48	50 +	60 +	70 +	80
Callitrichidae											
<i>Callitrix</i> <i>C. jacchus</i>						46					
<i>C. chrysolenca</i>						46					
<i>Cebuella</i> <i>C. pygmaea</i>					44						
<i>Saguinus</i> <i>S. illigeri</i>						46					
<i>Leontideus</i> <i>L. rosalia</i>						46					
<i>Callimico</i> <i>C. goeldii</i>							48				
Cercopithecidae											
<i>Cercopithecus</i>											
<i>C. aethiops</i>									60		
<i>C. diana</i>								58	60		
<i>C. neglectus</i>								58	62		
<i>C. mona</i>									66		
<i>C. cephus</i>									66		
<i>C. nictitans</i>									66		
<i>C. mitis</i>										70	
<i>C. lhoesti</i>										72	
<i>C. nigroviridis</i>									60	72	
<i>C. talapoin</i>											
<i>Erythrocebus</i>											
<i>E. patas</i>								54			
<i>Cercocebus</i> All species				42				54			
<i>Mandrillus</i> <i>M. sphinx</i>				42							
<i>M. leucophaeus</i>				42							
<i>Papio</i> All spp. (except											
<i>P. ursinus</i>)				42							
<i>Theropithecus</i>											
<i>T. gelada</i>				42							
<i>Macaca</i> All species				42							
<i>Cynopithecus</i>											
<i>C. niger</i>				42							
<i>Colobus</i> <i>C. polykomos</i>					44						
<i>Presbytis</i> <i>P. obscurus</i>					44						
<i>P. entellus</i>								50			
Hylobatidae											
<i>Hylobates</i> <i>H. lar</i> , <i>H. agilis</i>					44						
<i>H. booblock</i>					44						
<i>Symphalangus</i>											
<i>S. syndactylus</i>								50			
Pongidae											
<i>Pongo</i> <i>P. pygmaeus</i>							48				
<i>Pan</i> <i>P. troglodytes</i>							48				
<i>Gorilla</i> <i>G. gorilla</i>							48				
Hominidae											
<i>Homo</i> <i>H. sapiens</i>						46					

* Tentative data.

3. LONGEVITY RECORD IN CAPTIVITY†

<i>Alouatta</i>	3 yr 9 mo	<i>Indri</i>	—
<i>Anathana</i>	—	<i>Lagothrix</i> ¹⁴	12 yr 0 mo
<i>Aotus</i>	11 yr 7 mo	<i>Lemur</i>	27 yr 1 mo
<i>Arctocebus</i>	4 yr 6 mo	<i>Leontideus</i>	10 yr 4 mo
<i>Ateles</i> ¹²	20 yr 0 mo	<i>Lepilemur</i>	0 yr 3 mo
<i>Avahi</i>	—	<i>Loris</i>	7 yr 0 mo
<i>Brachyteles</i>	1 yr 8 mo	<i>Macaca</i>	29 yr 4 mo
<i>Cacajao</i>	8 yr 9 mo	<i>Mandrillus</i>	28 yr 6 mo
<i>Callicebus</i>	4 yr 2 mo	<i>Microcebus</i>	15 yr 5 mo
<i>Callimico</i>	2 yr 4 mo	<i>Nasalis</i> ⁵	4 yr 6 mo
<i>Callithrix</i> ¹	12 yr 0 mo	<i>Nycticebus</i>	12 yr 8 mo
<i>Cebuella</i> ¹²	4 yr 11 mo	<i>Pan</i> ⁶	41 yr 0 mo
<i>Cebus</i> ²	40 yr approx.	<i>Papio</i>	29 yr 10 mo
<i>Cercocebus</i>	20 yr 9 mo	<i>Perodicticus</i>	8 yr 11 mo
<i>Cercopithecus</i>		<i>Phaner</i>	—
(<i>Cercopithecus</i>)	31 yr 0 mo	<i>Pithecia</i>	13 yr 8 mo
(<i>Allenopithecus</i>)	8 yr 8 mo	<i>Pongo</i>	30 yr 8 mo
(<i>Miopithecus</i>)	22 yr 3 mo	<i>Presbytis</i> ⁷	20 yr 0 mo
<i>Cheirogaleus</i>	8 yr 8 mo	<i>Propithecus</i> ⁸	7 yr 0 mo
<i>Chiropotes</i>	15 yr 0 mo	<i>Ptilocercus</i>	—
<i>Colobus</i>		<i>Pygathrix</i>	0 yr 4 mo
(<i>Colobus</i>) ³	24 yr 0 mo	<i>Rhinopithecus</i>	—
(<i>Piliocolobus</i>)	2 yr 0 mo	<i>Saguinus</i>	
(<i>Procolobus</i>)	—	(<i>Saguinus</i>)	7 yr 6 mo
<i>Cynopithecus</i>	16 yr 7 mo	(<i>Oedipomidas</i>)	7 yr 8 mo
<i>Dendrogale</i>	—	(<i>Marikina</i>)	9 yr 10 mo
<i>Daubentonina</i> ⁴	3 yr 0 mo	<i>Saimiri</i> ⁹	21 yr 0 mo
<i>Erythrocebus</i>	20 yr 2 mo	<i>Simias</i>	—
<i>Galago</i>		<i>Symphalangus</i>	16 yr 2 mo
(<i>Galago</i>)	14 yr 0 mo	<i>Tarsius</i> ¹⁰	12 yr 0 mo
(<i>Galagoides</i>)	2 yr 10 mo	<i>Theropithecus</i>	10 yr 5 mo
(<i>Euoticus</i>)	—	<i>Tupaia</i>	
<i>Gorilla</i>	33 yr 5 mo	(<i>Tupaia</i>) ¹¹	5 yr 6 mo
<i>Hapalemur</i>	12 yr 1 mo	(<i>Lyonogale</i>)	2 yr 4 mo
<i>Hylobates</i>	31 yr 6 mo	<i>Urogale</i> ¹³	7 yr 0 mo

† Data from Jones (1962) unless otherwise stated.

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4. COMPARATIVE WEIGHTS OF PRIMATES

(Order based on heaviest weight of ♂)

	No. ♂♂	Grams	No. ♀♀	Grams
<i>Ptilocercus</i>	4	46 av.	—	—
<i>Tarsius</i>	10	95-165	8	87-154
<i>Tupaia glis</i>	—	177 av.	—	159 av.
<i>Galago senegalensis</i>	10	300 av.	9	229 av.
<i>Saguinus (Saguinus)</i>	3	264-341	4	264-395
<i>Loris</i>	16	85-348	7	85-270
<i>Urogale</i>	1	355	—	—
<i>Callithrix</i>	4	175-360	9	167-335
<i>Callimico</i>	—	472 av.	—	—
		(11 ♀♀ + 3 ♂♂)		
<i>Saguinus (Oedipomidas)</i>	5	300-510	3	337-567
<i>Leontideus</i>	1	553	1	480
<i>Callicebus</i>	1	681	—	—
<i>Aotus</i>	2	825, 1020	2	780, 1249
<i>Saimiri</i>	14	550-1135	5	365-750
<i>Galago crassicaudatus</i>	10	1241 av.	13	1034 av.
<i>Cercopithecus (Miopithecus)</i>	2	1230, 1280	2	745, 820
<i>Perodicticus</i>	2	1025, 1400	2	1000, 1200
<i>Pithecia</i>	6	1578 av.	5	1406 av.
<i>Nycticebus</i>	9	1012-1675	3	1105-1370
<i>Lemur</i>	3	2103 av.	2	1703, 2384
<i>Haplemur</i>	1	2625	1	2550
<i>Chiropotes</i>	2	2770, 3130	—	—
<i>Cebus</i>	18	1150-3320	—	—
<i>Colobus (Procolobus)</i>	7	3300-4400	5	2900-4100
<i>Cercopithecus (Cercopithecus)</i>	38	3178-6356	36	1816-3859
<i>Ateles</i>	2	5470, 6887	1	5824
<i>Simias</i>	—	—	1	7151
<i>Alouatta</i>	4	7392 av.	4	5720 av.
<i>Hylobates</i>	41	4300-7928	30	4110-6800
<i>Lagothrix</i>	7	3600-10,000	7	5000-6500
<i>Cynopithecus</i>	—	10,000-11,200	—	5100-7700
<i>Erythrocebus</i>	3	7483-12,600	4	4082-7100
<i>Brachyteles</i>	—	—	1	9500
<i>Symphalangus</i>	5	9500-12,700	5	9000-11,600
<i>Macaca</i>	87	3500-18,000	88	2500-16,300
<i>Mandrillus sphinx</i>	1	19,522	—	—
<i>Presbytis</i>	76	3650-20,884	79	3178-17,706
<i>Nasalis</i>	21	11,700-23,608	18	8165-11,794
<i>Theropithecus (estimated)</i>	1	20,500	1	13,620
<i>Papio</i>	—	22,000-30,000	—	11,000-15,000

	No. ♂♂	Grams	No. ♀♀	Grams
<i>Pan</i>	2	48,900 av.	4	40,600 av.
<i>Pongo</i>	4	69,000 av.	5	37,000 av.
<i>Gorilla</i> (estimated)	—	140,000-180,000	—	75,000-110,000

5. COMPARATIVE DIMENSIONS OF PRIMATES

(Order based on longest head and body length of male)

	No.	Sex	Head and body length (mm)	Tail length (mm)
<i>Microcebus murinus</i>	1	—	130	170
<i>Dendrogale</i>	9	♂♂	103-130	110-145
	7	♀♀	107-150	105-145
<i>Tupaia (Tupaia) minor</i>	25	♂♂	105-142	142-165
	19	♀♀	118-170	130-165
<i>Ptilocercus</i>	6	♂♂	120-143	165-180
	5	♀♀	120-140	170-180
<i>Cebuella</i>	6	—	130-144	197-210
<i>Tarsius</i>	9	♂♂	85-159	135-274
	14	♀♀	95-160	189-239
<i>Galago (Galagoides)</i>	—	—	125-160	182-199
<i>Galago (Galago) senegalensis</i>	10	♂♂	151-173	217-250
	10	♀♀	150-163	205-248
<i>Anathana</i>	5	♂♂	160-180	169-195
	3	♀♀	177-185	165-187
<i>Callimico</i>	2	♂♂	190, 215	255, 325
	1	♀	190	270
<i>Callithrix</i>	50	♂♂	173-220	243-375
	43	♀♀	158-240	247-385
<i>Tupaia (Tupaia) glis</i>	158	♂♂	140-230	129-215
	164	♀♀	143-225	130-205
<i>Urogale</i>	5	♂♂	182-235	148-170
	2	♀♀	200, 202	147, 150
<i>Galago (Euoticus)</i>	—	—	187-235	280-332
<i>Tupaia (Lyonogale)</i>	32	♂♂	161-240	145-196
	28	♀♀	175-240	140-190
<i>Saguinus (Oedipomidas)</i>	5	♂♂	219-245	362-382
	1	♀	250	370
<i>Microcebus coquereli</i>	—	—	250	280
<i>Arctocebus</i>	6	♂♂	220-251	8 approx.
	2	♀♀	231, 263	8 approx.
<i>Loris</i>	11	♂♂	186-264	—
	9	♀♀	198-249	—
<i>Cheirogaleus</i>	5	—	190-267	165-250
<i>Phaner</i>	—	—	250-275	325-350

	No.	Sex	Head and body length (mm)	Tail length (mm)
<i>Saguinus (Marikina)</i>	4	♂♂	219-292	349-368
	6	♀♀	210-250	235-420
<i>Saguinus (Saguinus)</i>	23	♂♂	170-310	275-420
	25	♀♀	155-280	325-425
<i>Avahi</i>	2	—	300, 330	390, 395
<i>Lepilemur</i>	3	—	280-356	254-280
<i>Leontideus</i>	6	—	227-370	300-360
<i>Cercopithecus (Miopithecus)</i>	1	♂	350	375
	2	♀♀	340, 370	360, 380
<i>Saimiri</i>	34	♂♂	249-370	367-465
	12	♀♀	225-295	370-445
<i>Hapalemur</i>	2	♂♂	365, 370	365
	3	♀♀	260-330	240-350
<i>Galago crassicaudatus</i>	4	♂♂	319-373	439-473
	4	♀♀	297-336	415-426
<i>Nycticebus</i>	15	♂♂	265-380	—
	14	♀♀	268-335	—
<i>Callicebus</i>	71	—	287-390	331-493
<i>Daubentonia</i>	—	—	400	560-600
<i>Perodicticus</i>	11	♂♂	337-406	50-81
	6	♀♀	355-417	56-72
<i>Chiropotes</i>	3	♂♂	400-407	380
	1	♀	460	350
<i>Lemur (except L. variegatus)</i>	11	—	303-456	370-560
<i>Aotus</i>	20	—	240-475	220-418
<i>Pithecia</i>	11	♂♂	355-480	315-510
	12	♀♀	300-425	255-545
<i>Colobus (Procolobus)</i>	8	♂♂	430-480	570-640
	6	♀♀	435-490	570-640
<i>Cacajao</i>	4	♂♂	435-485	155-185
	3	♀♀	365-445	150-165
<i>Cercopithecus (Allenopithecus)</i>	2	♂♂	460, 510	500, 525
	1	♀	410	355
<i>Propithecus</i>	4	—	458-534	483-560
<i>Simias</i>	3	♂♂	490-550	130-190
	3	♀♀	460-550	100-150
<i>Cebus</i>	77	♂♂	320-565	342-560
	51	♀♀	323-480	290-510
<i>Lagothrix</i>	58	♂♂	414-568	560-690
	51	♀♀	390-580	597-730
<i>Ateles</i>	17	♂♂	370-590	630-823
	30	♀♀	344-660	613-920
<i>Colobus (Piliocolobus)</i>	34	♂♂	455-610	550-800
	23	♀♀	470-600	412-790
<i>Lemur variegatus</i>	1	—	612	611

	No.	Sex	Head and body length (mm)	Tail length (mm)
<i>Cercocebus</i>	25	♂♂	515-615	690-940
	24	♀♀	435-580	590-895
<i>Brachyteles</i>	6	♂♂	462-630	650-741
	3	♀♀	470-565	740-800
<i>Hylobates</i>	62	♂♂	403-635	—
	38	♀♀	408-622	—
<i>Cercopithecus (Cercopithecus)</i>	107	♂♂	410-645	575-1090
	96	♀♀	315-520	480-1020
<i>Colobus (Colobus)</i>	37	♂♂	490-690	670-890
	28	♀♀	485-640	645-880
<i>Indri</i>	1	—	700	30
<i>Mandrillus leucophaeus</i>	1	♂	700	120
<i>Macaca</i>	115	♂♂	412-700	0-686
	81	♀♀	345-680	0-634
<i>Alouatta</i>	35	♂♂	465-720	490-748
	34	♀♀	390-573	490-711
<i>Nasalis</i>	11	♂♂	555-723	660-745
	4	♀♀	540-605	570-620
<i>Theropithecus</i>	2	♂♂	690, 740	460, 500
	2	♀♀	500, 650	325, 410
<i>Erythrocebus</i>	10	♂♂	575-750	620-740
<i>Papio</i>	5	♂♂	735-785	520-600
	4	♀♀	562-660	415-530
<i>Presbytis</i>	162	♂♂	415-787	495-1092
	131	♀♀	432-695	599-1016
<i>Cynopithecus</i>	4	♂♂	520-800	10-20
	4	♀♀	500-610	10-20
<i>Mandrillus sphinx</i>	1	♂	810	70
<i>Pygathrix</i>	6	♂♂	550-820	600-769
	2	♀♀	597, 630	597, 665
<i>Rhinopithecus</i>	7	♂♂	560-830	610-920
	5	♀♀	500-740	510-1040
<i>Symphalangus</i>	9	♂♂	468-846	—
	9	♀♀	460-630	—
<i>Pan</i>	7	♂♂	770-925	—
	4	♀♀	700-850	—
<i>Pongo</i>	7	♂♂	953 av.	—
	11	♀♀	777 av.	—

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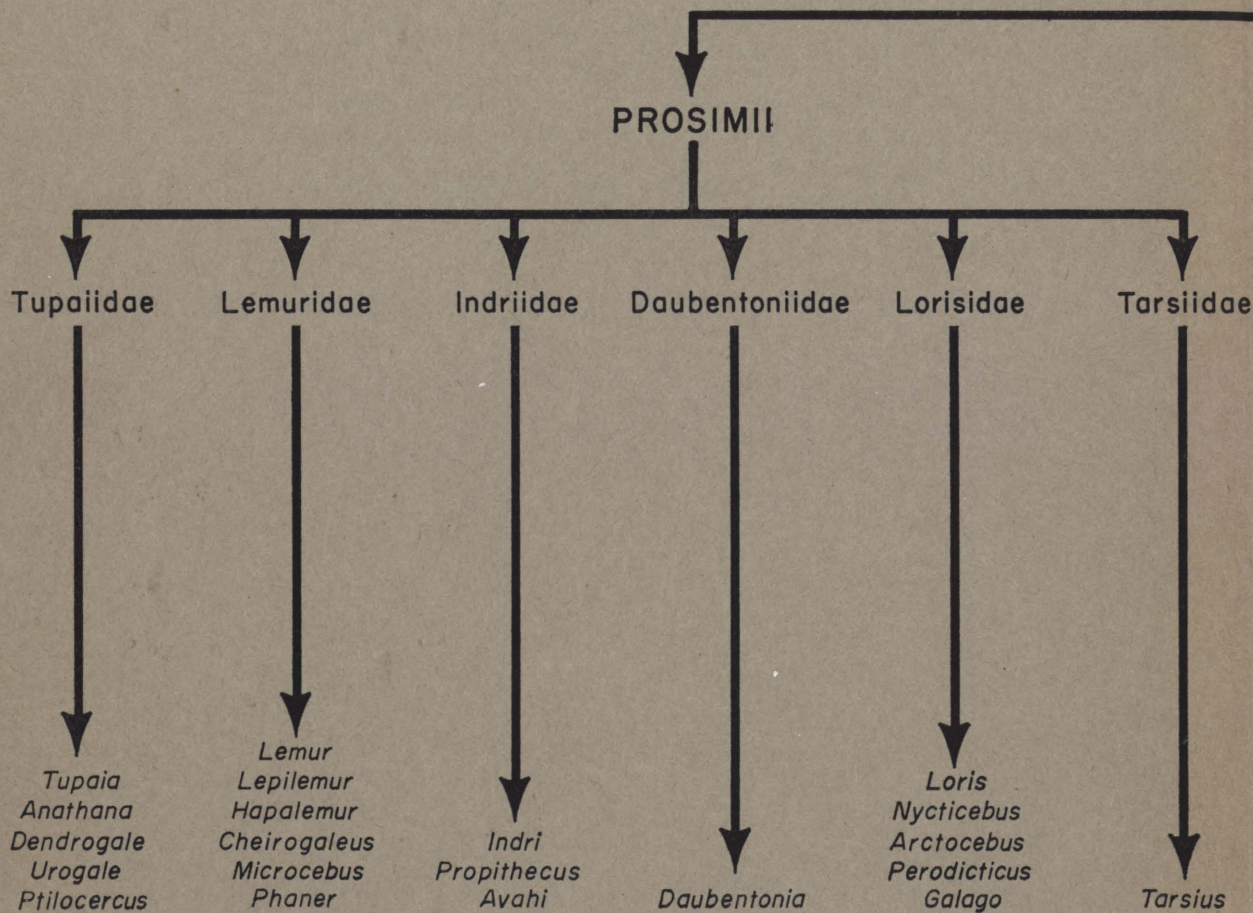
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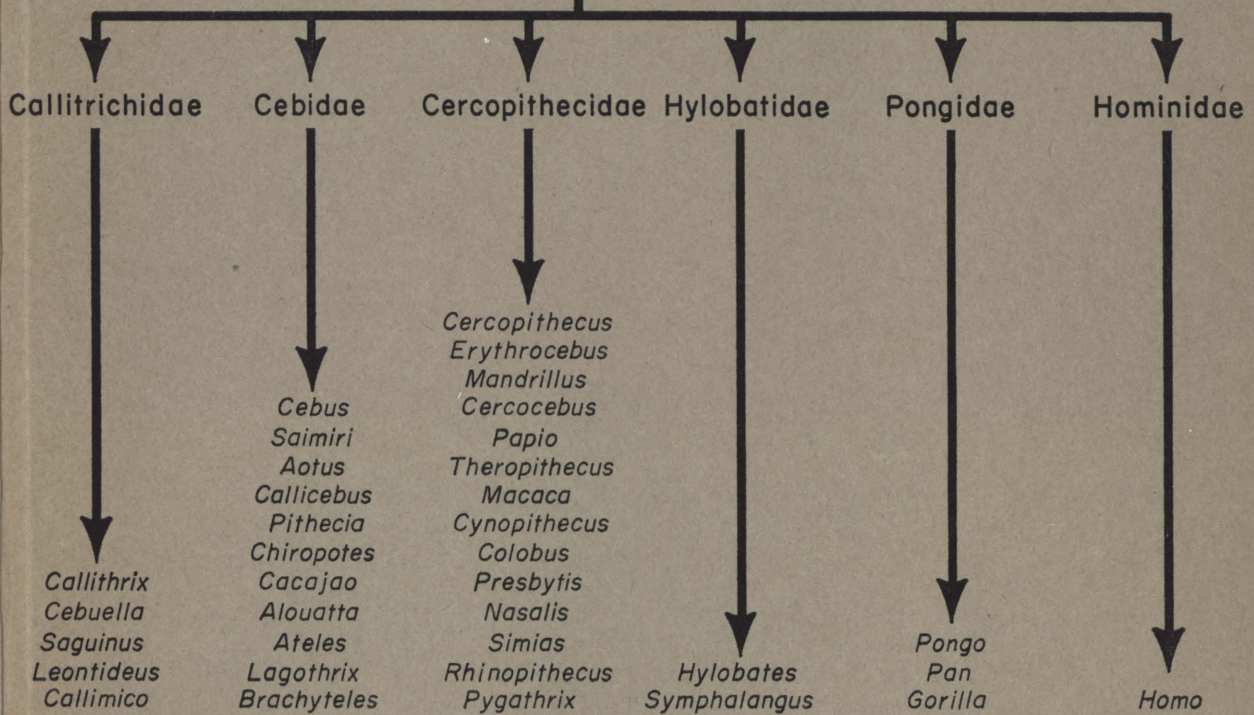
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